Neural Processing of Fearful and Happy Facial Expressions: Effects of Fixation to Facial Features and Task Demands

by

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A thesis

presented to the University of Waterloo

in fulfillment of the

thesis requirement for the degree of

Doctor of Philosophy

in

Psychology

Waterloo, Ontario, Canada, 2015

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AUTHOR'S DECLARATION

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners. I understand that my thesis may be made electronically available to the public.

Abstract

The current literature regarding the time course of facial expression processing is inconsistent and early emotion effects are debated. Facial expressions are well-known to be characterized by "diagnostic" facial features (e.g., the smiling mouth for happy expressions and wide open eyes for fearful expressions) and these "diagnostic" features have been suggested to modulate the neural response to facial expressions; however, a systematic investigation of the impact of facial features on the neural processing of facial emotions is lacking. Thus, in an attempt to elucidate the time course of facial expression processing, and these early emotion effects, the main objective of the current thesis was to investigate whether fixation to facial features influenced the neural response to facial expressions. Combining EEG and eye-tracking using a gaze-contingent procedure, three experiments tested whether fixation to the "diagnostic" facial features of a given emotion was driving these previously reported early emotion effects on well-known ERP components (P1, N170 and EPN) during a gender discrimination (Experiment -Exp.1), explicit emotion discrimination (Exp.2) and an oddball detection (Exp.3) task. Given that experimental procedures have also been highly inconsistent in the previous literature, the impact of task on the time course of facial expression processing was directly tested within-subjects in Exp.4. Differential effects for fearful and happy expressions were seen at posterior sites, earlier and mostly occipital for happy expressions and later and mostly lateral for fearful expressions with no differences seen between tasks (Exp.'s 1 to 4), and these emotion effects interacted with fixation to facial features (Exp.'s 1 to 3). Happy cues from the mouth were required for early processing of happy expressions (i.e., happy gist) likely driven by low-level differences and the

later semantic processing of the emotional content of the face. Fearful cues from both the mouth and the eyes were important for semantic processing of the emotional content of the face. Importantly, no interaction between emotion and fixation location was seen on the N170 (index of processing of structure of the face) arguing for separate processing of structural and emotional aspects of the face. Differential effects of fixation location were seen for the P1 and N170, with a sensitivity to face position (low-level) on the P1, followed by an eye sensitivity seen on the N170 component, possibly reflecting the activity of an eye-detector in the processing of the face structure. Overall, this thesis has helped to elucidate the debated early emotion effects in the temporal domain and has extended our current understanding of the role of facial features and task demands during facial expression processing. Results also highlighted the need for controlling for fixation in ERP emotion research and the importance of quantifying neural activity around P1 and N170 peaks as emotion effects may be missed by simply measuring these commonly studied ERP markers.

Acknowledgments

The research presented in this thesis was conducted at the University of Waterloo and was supported by a grant from the Natural Sciences and Engineering Research Council of Canada (NSERC CGS D Grant # 210825634).

I would like to sincerely thank my supervisor, Dr. Roxane Itier, for her guidance and support throughout this thesis, and especially for her confidence in me. She was patient and understanding but always pushed me to achieve my best whenever I was in doubt. Her expertise, professionalism and integrity has taught me so much about what it takes to become a research scientist. I could not have asked for a better role model and true friend.

I would also like to extend my gratitude to my thesis committee members, Dr. Michael Dixon and Dr. Daniel Smilek, for their insightful comments and suggestions which have been valuable additions to this thesis.

A very special thank you goes to my laboratory manager, Frank Preston, whose dedication, support, and readiness to help made my work so much smoother.

I also wish to thank my fellow lab members for their warm welcome, support, guidance, and valuable hints. To my office mates and colleagues, you are part of what makes me happy to start each day with a smile.

On a personal level I wish to thank my parents, grandparents, and the rest of my family, whose love and guidance is with me in whatever I pursue.

Finally, I express profound appreciation to my husband Brandon and step-daughter Ruby for their encouragement, understanding, and patience even during these hard times of study.

Dedication

This dissertation is dedicated to my parents. For their endless love, support and encouragement.

Thank you for giving me the strength to reach for the stars and always chase my dreams.

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Chapter 1: General Introduction

Our ability to perceive and recognize the emotional states and behavioural intentions of others is based to a large extent on the cues conveyed by facial expressions of emotion (hereafter facial expressions or facial emotions). The study of facial expressions dates back to at least the 19th century, as reflected in Charles Darwin's "The expression of emotions in man and animals" (Darwin, 1872), and remains one of the most active research areas in visual cognition to date. Certain facial expressions are universally recognized as signs of specific emotional states (Ekman, 1993; although see Jack, Garrod, Yu, Caldara, & Schyns, 2012). The most consistently expressed and recognized emotions include anger, fear, disgust, sadness and happiness (reviewed in Ekman 1999; see also Russell, Bachorowski, & Fernández-Dols, 2003). There has been a growing interest in how the brain processes emotional facial expressions and many studies have helped develop our understanding of the mechanisms that underlie facial emotion processing. While several studies have informed the literature on the cognitive (e.g., Calder, Young, Keane, & Dean, 2000; White, 2000) and neural processes (e.g., Adolphs, 2002a; Haxby, Hoffman, & Gobbini, 2002) involved in the perception and recognition of facial expressions, the findings from the current literature regarding the brain regions and time course of facial expression processing are inconsistent and several important questions remain. In this thesis, I present a series of studies conducted with the goal of elucidating the neural events underlying the extraction of information during the early visual stages of facial emotion processing.

1.1 Facial expressions and the role of facial features

Since the 1970's, Paul Ekman and colleagues have influenced research on facial expressions, reporting cross-cultural research on facial expressions that provides evidence for universality of basic emotions. Ekman's (1993) basic emotion model proposes that different emotions constitute discrete categories, with distinct evolutionary histories and independent neural circuits. Studies of brain responses to facial expressions of emotion therefore typically contrast different emotional categories, as specified by basic emotion models. The study of fearful expressions has dominated the facial expression literature. Researchers have shown a particular interest in fearful expressions because they convey a potential threat or danger and their rapid detection may be a crucial advantage for survival (Öhman, 2002). More recently research has begun to take interest in happy expressions, given that they are the most frequently encountered expressions in our everyday social communication. Fear and happiness are often compared as they present a comparison of threatening (avoidance) and non-threatening (approach) expressions, respectively (Lang, Bradley, & Cuthbert, 1997). Ideally, I would have included all six basic emotions in this thesis; however, due to practical constraints (i.e., experimental length) the present research will focus on these most commonly studied emotions, namely fearful and happy expressions.

Facial expressions are made up of specific configurations of facial muscle activity, often as an automatic emotional response (Kohler et al., 2004). These changes in facial musculature alter the facial features (e.g., wide open eyes in fear, upturned corners of the mouth in happiness). These facial configurations constitute species-specific universal expressions that are critical for proper social interaction and communication (Ekman, 1993). For instance, happy

expressions, characterized by a smiling mouth, signal that the person is open for communication and interaction. Recent studies have suggested that individual facial features may play a role during facial expression categorization, suggesting the importance of expression-specific facial features during the perception of facial emotions. Replicating earlier studies (e.g., Hanawalt, 1944) Calder and colleagues (2000; Experiment 1) demonstrated that the top half of the face was more important for accurate perception of fearful and angry expressions whereas the bottom half of the face was more important for accurate perception of happy expressions. Other evidence comes from visual scanning studies although the findings are somewhat mixed. Some studies have reported longer viewing times and more fixations towards the eyes compared to other features (i.e., nose and mouth) regardless of facial expression (e.g., Clark, Neargarder, & Cronin-Golomb, 2010; Guo, 2012; Sullivan, Ruffman, & Hutton, 2007), while other studies suggest fixations and viewing times may vary depending on the specific facial expressions. For example, Scheller, Büchel, and Gamer (2012) showed that participants made more saccades to the eyes compared to the mouth of fearful expressions and the opposite was seen for happy expressions. Eisenbarth and Alpers (2011) reported more saccades and fixations on the eyes for sad and angry faces, the mouth for happy faces, but equally for the mouth and eyes for fearful expressions. Using a response classification technique called *Bubbles* (Gosselin & Schyns, 2001) whereby portions of the face of various sizes and spatial frequencies are revealed, studies have suggested that specific locations of the face are most useful or diagnostic for the accurate discrimination of the six basic emotions (Smith et al., 2005). For example, the wide open eyes were the primary diagnostic cue for fearful expressions and the upturned corners of the smiling mouth for happy expressions. Following this, Neath and Itier (2014) tested the impact of fixation to expression-

specific facial features on the whole face. This was important given we interact mostly with whole faces in our everyday lives. Using a gaze-contingent procedure[1], we found that diagnostic facial features (like wide open eyes for fear) did not improve discrimination performance. Instead, results suggested the features are ''glued'' together (holistic processing) during the early stages of vision. Therefore, although there is growing support for the idea of a greater attention toward expression-specific diagnostic features, the role of facial features during facial expression recognition remains inconclusive. The current thesis attempts to clarify the role of facial features in the neural processing of fearful and happy expressions.

1.2 Cognitive and neural models of facial emotion perception

Arguably the most influential model of face perception was developed by Bruce and Young (1986). They proposed that the face processing system derives different types of information from facial stimuli that includes structural, identity and expression codes. They proposed that face processing begins with a "structural encoding" stage, where view-centered and abstract descriptions of global configuration and of features are extracted from the visual stimulus to support the analysis of expression and identity recognition. Expression and identity processing routes would start diverging right after the so-called "view-centered descriptions" of this structural encoding stage and remain segregated throughout subsequent processing stages.

A more recent model of face perception was suggested by Haxby, Hoffman and Gobbini (2000). Their model incorporates findings from functional neuroimaging and proposed a neural

[1] The gaze-contingent procedure is a relatively novel design that allows for precise control of where the participant is fixating on the facial stimulus. To achieve fixation on key facial features, a fixation cross is presented and participants are told to focus their attention on the cross and not to shift their gaze. If they shift their gaze the trial does not proceed. If the fixation cross was where the left eye of the face subsequently appeared, we can infer the person's gaze was focused on that left eye. If the fixation cross was where the mouth subsequently appeared, we can infer the person's gaze was on the mouth.

network for face processing, which consists of two main parts, the core system and the extended system. The core system contains three bilateral brain structures, the inferior occipital gyrus/"occipital face area" (IOG/OFA), the fusiform gyrus/"fusiform face area" (FG/FFA) and the superior temporal sulcus (STS). According to the model each of these structures has a different function: the IOG is involved in the early processing of facial features (e.g., Rossion et al., 2003), the FG processes invariant aspects of faces, such as identity or gender (e.g., Kanwisher, McDermott, & Chun, 1997), and the STS processes the variant aspects of faces, such as facial expressions (e.g., Allison, Puce, & McCarthy, 2000). The regions of the core system interact with one another and the FG and STS also send and receive input to the extended system. The extended system consists of the intraparietal sulcus (Cowan, 2011), the auditory cortex (Price, 2010), the amygdala, insula and the limbic system (Adolphs et al., 1999, 2002a, 2002b; Dolan & Vuilleumier, 2003), and the anterior temporal cortex (Gainotti, 2007). The amygdala in particular is thought to be involved in the emotional evaluation of faces and has many connections to the core system of face processing, primary visual cortex and prefrontal cortex, suggesting it might be involved in top-down influences on early visual processing (Palermo & Rhodes, 2007), although recent reviews suggest that the cortex has a more important role in emotion processing than was traditionally assumed (see Pessoa & Adolphs, 2010).

Both models of face perception reviewed (Bruce and Young, 1986; Haxby et al., 2000) suggest that the expression (is the person happy or angry) and identity of a face (is that Jane or Joan) are processed "by functionally and neurologically independent systems" (Calder & Young, 2005). However, in their review Calder and Young (2005) concluded that there is no study giving conclusive evidence for complete separation of these expression and identity processes. Along

the same lines, Vuilleumier and Pourtois (2007) reviewed the evidence from EEG and fMRI studies and concluded that emotional facial expression processing is too widely distributed in the brain to be only processed by the STS. They suggested that the FFA is sensitive to both emotional expression and identity (e.g., Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004), arguing against the idea that these two processes are completely independent.

Findings from investigations of the neural correlates underlying face perception have also led to the question of whether there are differentiable patterns of neural activity specific to each basic emotion (see Adolphs, 2002a for a review). In a recent meta-analysis, Vytal and Hamman (2010) reported that each of the basic emotions (fear, anger, surprise, happiness and sadness) were consistently associated with distinct and characteristic patterns of brain activity. For example, fear was consistently associated with amygdala activation, disgust with insula, amygdala and ventral prefrontal cortex, sadness with medial prefrontal cortex, anger with orbitofrontal cortex and happiness with rostral anterior cingulate cortex activation. However, in a more recent meta-analysis, every region that was activated for a given basic emotion was also activated for at least one other emotion (Lindquist, Wager, Kober, Bliss-Moreau, and Barrett, 2012). Thus, based on neuroimaging evidence it is unclear whether certain expressions preferentially draw upon specific brain regions, or if all expressions draw upon the same set of brain regions with different expressions having subtly different patterns of activation across these shared brain regions.

1.3 Face perception and ERP components

As reviewed above, neuroimaging research suggests that face perception may involve distinct brain regions. These regions may also become active in a specific time sequence and

therefore the complete understanding of face and facial expression perception also requires understanding their processing time course. In addition, it is unclear whether the brain distinguishes emotional from neutral facial expressions in general or distinguishes among different emotions (i.e., specialized processing of fearful expressions). Event-related potentials (ERPs), a specific type of analysis of electroencephalographic (EEG) data, are a useful tool that enables the assessment of neural responses to affective events with millisecond temporal resolution and complements findings from neuroimaging studies about the face neural network in the temporal domain. ERPs allow us to examine whether structural and emotional aspects of face encoding are independent or interacting processes and when the brain distinguishes between emotional expressions by linking these cognitive processes with neural activity and specific ERP components defined by a specific time course and scalp topography (Kappenman & Luck, 2012).

1.3.1 The visual P1 component

The first visual ERP investigated in face perception is the visual P1 occurring ~80-120ms post-stimulus onset and typically maximum at occipital sites. The P1 is thought to be generated within extrastriate visual cortex (V2, V3 and posterior fusiform gyrus) (Clark, Fan, & Hillyard, 1995). This component is known to be sensitive to attention (Luck, 1995; Luck, Woodman, & Vogel, 2000; Mangun, 1995) and low-level stimulus properties such as colour, contrast, luminance and spatial frequencies (Johannes, Münte, Heinze & Mangun, 1995; see Regan, 1989, cited by Rossion and Jacques, 2012). While early studies suggested P1 might reflect the earliest timing of face-specific effects, recent studies converge to support the idea that face-object differences seen on PI component are likely due to low-level factors (e.g., Ganis, Smith, &

Schendan, 2012; Jemel et al., 2003; Rossion & Caharel, 2011; Tarkiainen, Cornelissen, & Salmelin, 2002; Rousselet, Husk, Bennett, & Sekuler, 2008), a finding recently confirmed by unmixing of the components underlying the P1 and N170 (Desjardins & Segalowitz, 2013)..

A growing number of studies have now reported enhanced P1 amplitude for fearful relative to neutral faces (e.g., Batty & Taylor, 2003; Jetha, Zheng, Schmidt, & Segalowitz, 2012; Pourtois, Grandjean, Sander, & Vuilleumier, 2004; Sato, Kochiyama, Yoshikawa, & Matsumura, 2001; Smith, Weinberg, Moran, & Hajcak, 2013; Wijers & Banis, 2012). This early fearful effect has been interpreted as reflecting the greater activation of early visual brain areas to intrinsically salient, threat-related stimuli, via the activation of a subcortical route involving the amygdala (see Vuilleumier & Pourtois, 2007 for a review). Fearful faces would automatically engage this subcortical structure which, in turn, would modulate and enhance cortical processing of the face stimuli (Morris et al., 1998; Vuilleumier et al., 2004; Whalen et al., 1998). This cortical modulation would result in variations of the neural activity recorded on the scalp with ERPs. Because of its early timing, which corresponds to the activation of early visual areas rather than higher-order visual areas, this effect is thought to reflect a coarse emotion extraction, the "threat gist" (e.g., Luo, Feng, He, Wang, & Lu, 2010; Vuilleumier & Pourtois, 2007), that might rely on low spatial frequencies (Vuilleumier et al., 2003). A more elaborated processing of the visual threat would occur later, around or after the N170 (e.g., Luo et al., 2010), the ERP component most studied in face perception. It is important to note that this early P1 modulation by emotion is currently debated and several studies have reported no modulation of the P1 by emotion (see Vuilleumier & Pourtois, 2007 for a review). In many of these studies low-level visual features of stimuli (e.g.,

luminance) were not controlled for (e.g., Batty & Taylor, 2003) and might have driven these early reported responses.

1.3.2 The face-sensitive N170 component

It is generally agreed that the earliest reliable neural signature of face perception is detected in the EEG about 170 milliseconds after stimulus presentation, and manifests as a negative ERP component (N170) over occipito-temporal electrode sites ~130-200ms post-stimulus onset (e.g., Bentin, Allison, Puce, Perez, & McCarthy, 1996; Ganis, Smith, & Schendan, 2012; Jemel et al., 2003; Rossion et al., 2000; Rossion & Caharel, 2011). This component is thought to reflect encoding of the structure of the face (Bentin et al., 1996; Bentin & Deouell, 2000; Eimer, 2000; Itier & Taylor, 2002, 2004; Rossion et al., 2000) and to thus correspond roughly to the structural encoding stage of Bruce and Young (1986). The bulk of the literature supports the view that it reflects holistic processing, the integration of facial features into an indecomposable whole (Rossion, 2009; but see Nemrodov, Anderson, Preston, & Itier, 2014 and Zheng, Mondloch, Nishimura, Vida, & Segalowitz, 2011). ERP research has suggested the FG (Itier & Taylor, 2002; Itier et al., 2006; Rossion et al., 1999; Rossion et al., 2003) and STS (Itier et al., 2007; Itier and Taylor, 2004) as potential generators of the N170 although the IOG has also been proposed (for a review see Rossion & Jacques, 2011).

Like the P1, reports of the N170 sensitivity to facial emotions have been inconsistent. A number of studies have reported larger N170 responses to emotional faces, especially fearful expressions, compared to neutral faces (e.g., Batty & Taylor, 2003; Blau, Maurer, Tottenham, & McCandliss, 2007; Caharel, Courtay, Bernard, Lalonde, & Rebaï, 2005; Leppänen, Moulson, Vogel-Farley & Nelson, 2007; Leppänan, Hietanen, & Koskinen, 2008). However, as seen for the P1, a

lack of sensitivity to facial expressions of emotion has also been reported for the N170 component in many studies (e.g., Ashley, Vuilleumier, & Swick, 2004; Balconi & Lucchiari, 2005; Herrmann, Aranda, Ellgring, Mueller et al., 2002; Krolak-Salmon, Fischer, Vighetto, & Mauguière, 2001; Münte, Brack, Grootheer, Wieringa et al., 1998; Pourtois et al., 2005; Shupp, Junghöfer, Weike, & Hamm, 2004; Smith, Weinberg, Moran, & Hajack, 2013). In a very recent meta-analysis, Hinojosa, Mercado and Carretié (2015) attempted to resolve the inconsistencies surrounding the sensitivity of N170 to emotions. Out of 128 possible studies testing the N170 and emotion, they analyzed 57 studies and reported the N170 to be indeed sensitive to facial expressions. The results also suggested that the N170 is more sensitive to particular facial expressions and less, or not at all, to others. In particular, the meta-analysis revealed that the greatest effect sizes corresponded to fearful>neutral and angry>neutral contrasts, followed by the happy>neutral contrast. However, disgusted>neutral and sad>neutral contrasts did not reach significance.

As the N170 is thought to reflect structural encoding stages, sensitivity of this component to facial emotion is usually interpreted as reflecting a sensitivity to the variations in the structure of the face by the facial expression (i.e., changes in shape of the various facial features; see Vuilleumier and Pourtois, 2007) rather than the full appraisal of the emotion *per se*. Others interpret the N170 variations with emotion as reflecting an integration of expression and identity processing (e.g., Hijonosa et al., 2015). A better demonstration of a true integration of identity and expression, however, requires showing an interaction between the processing of face identity *per se* and that of facial emotion, by using different task demands on the same stimuli. This has been demonstrated in neuroimaging studies (e.g., Fox, Moon, Iaria, & Barton, 2009; but see Winston, Henson, Fine-Gould, & Dolan, 2004) and neuropsychological case studies (Calder &

Young, 2005; but see Bate & Bennetts, 2015) but research using ERPs is lacking. One way to test for this potential integration is to test for an interaction between the processing of a facial feature, which is integrated into the face percept during structural encoding at the level of the N170, and facial expressions.

1.3.3 The Early Posterior Negativity (EPN)

Another well studied ERP in facial expression research is the well-known marker of emotion processing Early Posterior Negativity (EPN), a negative potential measured over occipito-temporal sites ~150-350ms post-stimulus onset. The EPN is enhanced for emotional relative to neutral stimuli, for both verbal and non-verbal material including faces (Rellecke, Palazova, Sommer, & Schacht, 2011; Schupp et al., 2003, 2004). Like the N170, the EPN is commonly reported to be most pronounced for threat-related expressions (i.e., fearful and angry expressions) compared to neutral and happy expressions (e.g., Rellecke et al., 2011; Schupp et al., 2004) although there are reports of a general emotion effect with more negative amplitudes for both threatening and happy expressions compared to neutral expressions (Sato et al., 2001; Schupp, Flaisch, Stockburger, & Junghöfer, 2006). Therefore this effect has been suggested to reflect enhanced processing of emotionally salient faces in general, and of threatening faces (i.e., fearful and angry) in particular, in cortical visual areas (Schupps et al., 2004).

The current view is that the EPN reflects more in depth appraisal of the emotion, some form of semantic stage where the meaning of the emotion is extracted (Vuilleumier and Pourtois, 2007; Luo et al., 2010). Some studies have suggested that the EPN reflects the neural activity related to the processing of the emotion that is added onto the normal processing of the face. This added activity would sometimes start around the N170 and be responsible for the emotional

effects reported for the N170 (Leppänen et al., 2008; Rellecke et al., 2013; Schupps et al., 2004), although it seems largest *after* the N170. According to this interpretation, structural encoding, as indexed by the N170, and facial emotion encoding, are separate processes and the emotion effect is just more or less strong depending on the emotion.

1.4 (Expressionless) Face perception and facial features assessed by ERPs

Two recent studies controlling for fixation position using an eye-tracker and a gaze-contingent procedure have shown that the N170, until now believed to reflect face holistic processing, is also sensitive to features within the face and in particular to the eyes. Larger N170s were indeed reported for fixation on the eyes compared to fixation on the mouth of upright faces (de Lissa et al., 2014; Nemrodov et al., 2014; see also Zerouali, Lina, & Jemel, 2013) or compared to fixation on the nose, forehead and even nasion (Nemrodov et al., 2014). This finding echoes previous reports of larger N170s for eye regions presented in isolation compared to whole upright faces (Bentin et al., 1996; Itier, Latinus, & Taylor, 2006; Itier, Alain, Sedore, & McIntosh, 2007; Itier, Van Roon, & Alain, 2011; Taylor, Edmonds, McCarthy, & Allison, 2001) and larger N170s for facial characteristics including eye color and size (Zheng et al., 2011), confirming a special role for eyes in the early processing of the face structure, as also suggested by response classification techniques (e.g., Rousselet, Ince, van Rijsbergen, & Schyns., 2014; Schyns et al., 2003, 2007, 2009). Importantly however, these recent eye-tracking-EEG studies demonstrated the sensitivity of the N170 to eyes in full faces when the face configuration was not altered (configuration is altered with presentation of isolated eyes or when portions of faces are revealed as in the response classification technique *Bubbles*). In addition, Nemrodov et al. (2014) showed that this eye sensitivity disappeared in eyeless faces, demonstrating it was due to the presence

of the eyes at fovea. These findings, along with numerous others, led the authors to develop the Lateral Inhibition Face Template and Eye Detector (LIFTED) model which proposes that the N170 reflects both the activity of an eye-detector and the processing of a face as a whole in a complex interplay between information at fovea and information in parafovea (Nemrodov et al., 2014). In addition to providing a new theoretical account of holistic and featural processing at the neural level, this study highlights the importance of controlling for fixation to face features in ERP face research. In the present thesis, the same gaze-contingent approach was used in the study of facial expressions of emotion, which constitutes, to the best of my knowledge, the first work of its kind in that domain.

1.5 Facial expression perception and facial features assessed by ERPs

Spatial attention to the face plays an important role during the processing of facial emotions (e.g., Holmes, Kiss, & Eimer, 2006; Wijers & Banis, 2012). In fact, differences in the amount of attention devoted to the emotional face may be one reason for inconsistencies in reports of early emotion effects on P1 and N170. Emotion effects on these components were indeed eliminated when attention was covertly directed away from the foveally presented emotional faces towards other faces in the periphery (Wijers & Banis, 2012) or towards vertical lines flanking the emotional faces (Holmes et al., 2006). Another factor possibly contributing to these inconsistent early ERP effects of emotion is the differing amount of attention to facial features.

The role of facial features in the neural response to facial expressions has recently been investigated in ERP research but remains unclear. Research using the *Bubbles* technique in combination with ERPs has suggested that the eye region provides the most useful diagnostic

information for the recognition of fearful facial expressions and the mouth for the recognition of happy facial expressions. A three-stage model was proposed whereby the face-sensitive N170 is characterized by the encoding of the expression-specific diagnostic featural information (Schyns et al., 2007, 2009). Facial information extraction begins at the eye (locally) irrespective of facial expression, followed by a more global processing of facial information, and finally zooms back in to locally encode the feature diagnostic for discriminating a particular expression. When the feature diagnostic for the discrimination of that emotion has been detected, the N170 peaks (Schyns et al., 2007).

Also supporting the importance of fearful eyes, Leppänen et al. (2008) reported that an early fearful effect, seen as more negative amplitudes for fearful compared to neutral faces from the peak of the N170 (~160ms in that study) until 260ms (encompassing the visual P2 and EPN), was eliminated when the eye region was covered, demonstrating the importance of this facial area in the neural response to fearful expressions. Calvo and Beltrán (2014) reported hemispheric differences in the processing of facial expressions using face parts and whole faces. An enhanced N170 in the left hemisphere was seen for happy compared to angry, surprised and neutral faces for the bottom face region presented in isolation (including the mouth), but not for the top face region presented in isolation (including the eyes), or for the presentation of the whole face. In the right hemisphere in contrast, the N170 was enhanced for angry compared to happy, surprised and neutral faces for whole faces only. Taken together these studies suggest that the expression-specific diagnostic features modulate the neural response to facial expression at the level of the N170 or later.

All these ERP studies have employed techniques that forced feature-based processing by revealing facial information through apertures of various sizes and spatial frequencies (e.g., *Bubbles,* Schyns et al., 2007, 2009), by presenting isolated face parts (Calvo & Beltrán, 2014; Leppänen et al., 2008) or by covering portions of the face (Leppänen et al., 2008). The bulk of the literature on face perception, however, supports the idea that faces are processed holistically, whether the focus is on identity (McKone, 2008; Rossion & Jacques, 2008) or emotion (Calder & Jansen, 2005; Calder et al., 2000) recognition. Moreover, components such as the N170 have been shown to be very sensitive to disruption of this holistic processing (Itier, 2015; Rossion and Jacques, 2011, for reviews). A systematic investigation of the impact of facial features on the neural processing of facial emotion in the context of the whole face is lacking. This is important given we almost invariably encounter whole faces in our daily social interactions, and eye-tracking studies suggest that faces are explored and that fixation moves across facial features, with a larger exploration of the eyes (see Itier, 2015, for a review). By using a gaze-contingent approach, the present thesis attempts to fill this gap.

1.6 Overall thesis aims

The previous literature regarding the time course of facial expression processing is inconsistent and early emotion effects are debated. In an attempt to elucidate the time course of facial expression processing, and these early emotion effects, the main aim of this thesis was to investigate whether fixation to facial features influenced the neural response to facial expressions. Using a gaze-contingent procedure with an eye-tracker to enforce fixation combined with EEG recordings, I tested whether fixation to facial features suggested to be "diagnostic" for a given emotion was driving previously reported early emotion effects on well-known ERP

components (P1, N170 and EPN). Diagnostic features have been suggested to vary as a function of task demands (Schyns, Bonnar, & Gosselin, 2002); therefore, this hypothesis was tested during gender discrimination (Exp.1), explicit emotion discrimination (Exp.2) and oddball detection (Exp.3) tasks. This experimental paradigm also allowed me to test whether processing of structural and emotional aspects of faces are independent or interact. Facial features are integrated into the face percept during structural encoding (at the level of the N170 ERP component) and an interaction of fixation with a given facial expression at the N170 would imply an integration of face and emotion processing. Lack of an interaction would imply separate processing of these aspects. Finally, experimental procedures have been highly inconsistent in the previous literature; however, the effect of task remains unclear. In Exp. 4 I directly tested the impact of task demands on the time course of facial expression processing.

Chapter 2: Fixation to features and neural processing of fearful and happy facial expressions in a gender discrimination task[2] (Exp.1)

2.1 Introduction

The N170 is arguably the first face-sensitive ERP component, measured over the scalp at occipito-temporal sites ~130-200ms after stimulus-onset, and reflects structural encoding of the face (e.g., Bentin, Allison, Puce, Perez, & McCarthy, 1996; Ganis, Smith, & Schendan, 2012; Jemel et al., 2003; Rossion et al., 2000; Rossion & Caharel, 2011). Whether the N170 is also sensitive to facial emotions is a matter of ongoing debate as results have been inconsistent in the previous literature (Vuilleumier & Pourtois, 2007). Several studies have reported an increased N170 response to facial expressions, most commonly for fearful faces compared to neutral faces (e.g., Batty & Taylor, 2003; Blau, Maurer, Tottenham, & McCandliss, 2007; Caharel, Courtay, Bernard, Lalonde, & Rebaï, 2005; Leppänen, Moulson, Vogel-Farley, & Nelson, 2007; Leppänan, Hietanen, & Koskinen, 2008). However, many others have reported no modulation of the N170 by facial emotion (e.g., Ashley, Vuilleumier, & Swick, 2004; Balconi & Lucchiari, 2005; Herrmann, Aranda, Ellgring, Mueller et al., 2002; Krolak-Salmon, Fischer, Vighetto, & Mauguière, 2001; Münte, Brack, Grootheer, Wieringa et al., 1998; Pourtois et al., 2005; Smith, Weinberg, Moran, & Hajcak, 2013).

The eye region is used most prominently when discriminating fear from other expressions (Smith, Cottrell, Gosselin, & Schyns, 2005) and eyes have been shown to convey threat even when presented in isolation (Fox & Damjanovic, 2006; Whalen et al., 2004). Recently, it has been shown that participants make spontaneous saccades towards the eyes of emotional

[2] A version of this chapter was originally published in *Brain and Cognition* (Neath & Itier, 2015)

faces presented even for as short as 150ms (Gamer, Schmitz, Tittgemeyer, & Schilbach, 2013). Given that previous ERP studies reporting modulations of the N170 with fearful faces did not use an eye-tracker to confirm gaze position, and that the eyes are salient in fearful faces, it is possible that the participants made small eye movements towards the eyes or attended to the eyes more for fearful faces than other expressions. These possible movements to the eyes may be responsible for the modulations of the N170 by fearful expressions reported previously in the literature. In Exp.1, I tested this hypothesis by manipulating fixation to specific features of facial expressions using a gaze-contingent procedure.

As the use of gaze-contingent procedures is very new in ERP face research, I also aimed to investigate more thoroughly the effect of fixation to features, in particular the sensitivity to the eyes, on other ERP components than the N170, namely the preceding P1 and the following Early Posterior Negativity (EPN) components. P1 is a positive component occurring ~80-120ms at occipital sites and is known to respond to the low-level characteristics of stimuli such as contrast, luminance, colour and spatial frequencies (Rossion & Jacques, 2008) and is also sensitive to attentional effects (Luck, Woodman, & Vogel, 2000; Mangun, 1995). However, it is unclear whether the P1 is sensitive to fixation to features and especially to eyes, and its sensitivity to emotional expressions has been controversial (see Vuilleumier & Pourtois, 2007 for a review). The EPN, beginning at ~150ms and largest between ~200-350ms at occipital-temporal sites, is a well-known marker of emotion processing with a more negative-going response for threatening faces (i.e., angry and fearful faces) compared to happy and neutral expressions (e.g., Rellecke, Sommer, & Schacht, 2013; Rellecke, Palazova, Sommer, & Schacht, 2011; Schupp, Junghöfer, Weike, & Hamm, 2004). No study to date has investigated whether EPN could be preferentially

modulated by attending to specific facial features bearing emotional significance such as the eyes in fearful faces or the mouth in happy faces.

I investigated whether fixation to the eyes (and mouth) of fearful, happy and neutral faces modulates P1, N170 and EPN responses. Faces were presented with fixation locations on the left eye, right eye, nose and mouth during a gender discrimination (GD) task. To ensure correct point of gaze, eye-tracking was used with a fixation-contingent stimulus presentation and any trial in which gaze deviated by more than 1.4° of visual angle around that fixation location was excluded. To further prevent participants from using anticipatory strategies the fixation-cross was always presented in the center of the screen, while faces were moved around to obtain fixation on the desired feature, as done in Nemrodov et al. (2014) and de Lissa et al (2014). Given this experimental manipulation we expected an interaction between eye fixation location and hemisphere for the P1 amplitude as most of the face was situated in the left hemifield when fixation was on the right eye (the eye situated on the right side of the participant) and in the right hemifield when fixation was on the left eye (e.g., Luck, Heinze, Mangun, & Hillyard, 1990). I also expected to replicate Nemrodov et al.'s findings (2014) of a larger N170 response for fixation on the eyes compared to fixation on the nose and mouth. Crucially, if attention to the eyes was driving the previously reported N170 increase for fearful faces, I expected to see an emotion by fixation interaction with an enhanced N170 response for fearful faces only when fixation was on the eyes. Alternatively, if emotional expressions are processed holistically (Bimler, Swarek, & Paramei, 2013; Derntl, Seidel, Kainz, & Carbon, 2009; McKelvie, 1995), and no particular feature is any more important than any other feature for a given emotion then we expected to see a larger N170 response to fearful faces irrespective of fixation location. Finally, the possibility

remained that no modulation of the N170 by emotion would be found but I expected a modulation of the EPN, a classic marker of emotion, with a more negative-going response for fearful compared to happy and neutral faces as reported previously (e.g., Schupp et al., 2004). Whether EPN could also respond more to fixation on the eyes of fearful faces than to fixation on other facial features was unpredictable although the fact that EPN was sensitive to emotion even when eyes were covered (Leppänen, Hietanen & Koshinen, 2008) led to the prediction that fixation on the eyes would not matter at this stage.

2.2 Methods

2.2.1 Participants

Forty-nine undergraduate students from the University of Waterloo (UW) were recruited and received course credit for their participation. All participants lived for at least 10 years or more in North America and reported normal or corrected-to-normal vision as well as no history of neurological or psychiatric disorder. Informed consent was obtained before starting the experiment and the study was approved by the Research Ethics Board at UW. For ten participants, their eye fixations could not be captured by the eye-tracker during calibration. These participants were therefore not tested. Of the 39 participants tested, 19 were rejected for the following reasons. To ensure overt attention to the fixated feature, trials with fixations greater than 1.4° of visual angle from the fixation location (see procedure below) were removed. For eleven participants, this procedure put the overall number of trials below our cut-off score of 40 (correct) trials per condition (i.e., less than 50% of the trials), for multiple conditions. These

11 participants were thus removed[3]. Five participants were rejected due to too many artefacts also resulting in too few trials per condition. Finally, three were rejected due to high anxiety scores. Anxiety is known to interact with the processing of emotions like fear (e.g., Dugas, Gosselin, & Ladouceur, 2001); therefore, only participants with scores in the normal range below 43 on the State-Trait Inventory for Cognitive and Somatic Anxiety questionnaire (STICSA; Ree, French, MacLeod, & Locke, 2008; Van Dam, Gros, Earlywine, & Antony, 2013), were included. The remaining 20 participants (8 females, 18-23 years, *M* = 20.06 years) were included in the data analyses.

2.2.2 Stimuli

Photographs of 8 individuals (4 males, 4 females) each with fearful, happy and neutral expressions were selected from the MacBrain Face Stimulus Set[4] (Tottenham et al., 2009). Images were converted to grayscale in Adobe™ Photoshop CS5 and an elliptical mask was applied on each picture so hair, ears and shoulders were not visible. All faces subtended a visual angle of 6.30° horizontally and 10.44° vertically, and were presented on a gray background for an image visual angle of 9.32° horizontally and 13.68° vertically (see Fig.1). Images did not differ significantly in RMS contrast and pixel intensity between emotions (see analyses and result sections below).

[3] Note that this high attrition rate indirectly shows that many participants make many eye movements even with 257ms presentation times and that, although tiny, these eye movements are sufficient to put fixation on another facial feature given the size of the stimuli.

[4] Development of the MacBrain Face Stimulus Set was overseen by Nim Tottenham and supported by the John D. and Catherine T. MacArthur Foundation Research Network on Early Experience and Brain Development. Please contact Nim Tottenham at tott0006@tc.umn.edu for more information concerning the stimulus set. The models used in the present study were models # 2, 3, 6, 8, 20, 24, 33, 34

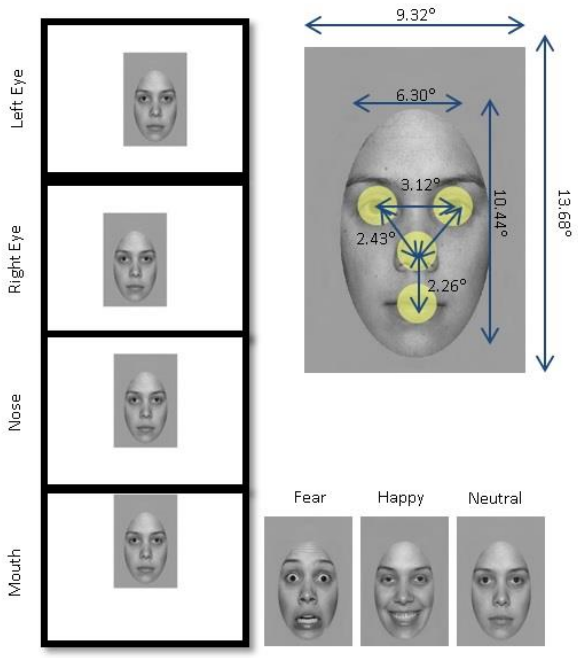


Figure 1. Stimulus and Fixation Location Example

Left panel: examples of one neutral face presented at each fixation location. Participants fixated in the center of the monitor represented here by each rectangle and the face was presented offset so that gaze fixated four possible face locations: left eye, right eye, nose and mouth. Note that eye positions are from a viewer perspective (i.e., left eye is on the left of the image). This resulted in the face situated almost entirely in the upper visual field when fixation was on the mouth, mostly in the left visual field when fixation was on the right eye, and mostly in the right visual field when fixation was on the left eye. Right panel, up: one neutral face exemplar with picture size and angular distances between fixation locations (averaged across all emotions and face identities). The yellow circles represent the interest areas of 1.4° centered on each feature that were used to reject eye gaze deviations in each fixation condition (i.e., foveated areas which did not overlap) and to calculate local RMS contrast and pixel intensity for each picture. Right panel, bottom: exemplars of fearful, happy and neutral expressions used in the present study (from NimStim database). Note that this design and the faces used were identical across Exp.'s 1-3.

For each stimulus, exact coordinates corresponding to 4 feature locations on the face were recorded: left eye, right eye, nose and mouth. Please note that in this experiment, and in the remainder of this thesis, fixation positions are from a viewer perspective so that the left eye of the face is to the viewer's left, and the right eye is on their right. Fixation-crosses on the nose and mouth were aligned with one another along an axis passing through the middle of the nose and face. Eye coordinates were determined by placing the cross on the center of the pupil. A

unique central fixation-cross was used and each face was presented offset so the predetermined center of each feature would land on the center of the fixation-cross (Fig.1). No picture was presented in the exact same location due to minor variations in the coordinates of each feature between the eight identities and the three expressions used.

2.2.3 Apparatus and Procedure

Participants sat in a sound-attenuated Faraday-cage protected booth 70cm from a Viewsonic P95f+ CRT 19-inch colour monitor driven by an Intel Quad CPU Q6700 with a refresh rate of 75Hz. Participants performed a gender discrimination task using a game controller to record their responses. For half the participants, they pressed the left key for depictions of male faces, the right key for female faces. For the other half they pressed the right-key for males, left key for females. Before the experiment started, participants were given an 8 trial practice session to introduce them to the experimental procedure. Each trial began with a 0-107ms jittered fixation-cross. Participants were instructed to fixate on the black centered fixation-cross to initiate the trial and to remain fixated there until the response screen appeared. To ensure that participants were fixating on the fixation-cross, a fixation-contingent trigger enforced the fixation on the cross for 307ms[5]. The face stimulus was then presented for 257ms, followed by a white screen with a question mark prompting their response. This response screen was presented until the participant responded, or for a maximum of 907ms (Fig.2). On average it took participants 621ms (118ms S.D.) to respond (RTs were calculated from face onset; see Table 3). Participants were instructed to categorize faces by their gender as quickly and accurately as possible. After

[5] In practice, it took a bit of time for participants to be correctly fixated on the fixation trigger for a minimum of 307ms, resulting in an average of 964ms (1214ms S.D) between the first onset of the fixation cross and the onset of the stimulus presentation. When this time exceeded 10s, a mid-block calibration was done again.

their response, a screen appeared that read “BLINK” for 507ms. Participants were instructed to blink during this time to prevent as much as possible eye movement artifacts during the first 500ms of trial recording. If the participant did not respond, or responded during the “blink” screen, the trial was considered a “miss” and was eliminated from further analysis.

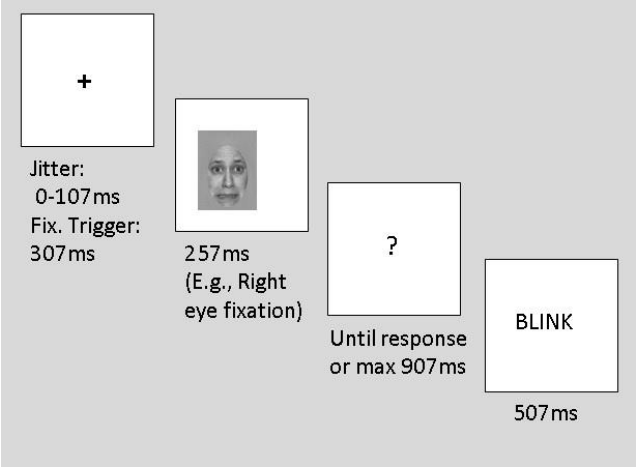


Figure 2. Gender Discrimination Trial Sequence (Exp.1)

Trial example with right eye fixation: Participants were tested on 960 trials as follows. First the fixation point was displayed on the screen for a jittered amount of time (0-107ms) with a fixation trigger of 307ms. Then the grayscale picture was flashed for 257ms, immediately followed by a white screen with a question mark for 907ms during which participants indicated their response. Lastly, a blink screen appeared for 507ms.

The block of 96 face trials (3 emotions X 4 fixation locations X 8 identities) was repeated 10 times with a different trial order (randomized), yielding 80 trials per condition across blocks, for a total of approximately 1.5 hours of testing time. Participants then completed the 21-item of the trait test from the State-Trait Inventory for Cognitive and Somatic Anxiety (STICSA; Ree, French, MacLeod, & Locke, 2008). The STICSA is a Likert-scale assessing cognitive and somatic symptoms of anxiety as they pertain to one’s mood in general.

2.2.4 Electrophysiological Recordings

The EEG recordings were collected continuously at 516Hz by an Active-two Biosemi system at 72 recording sites: 66 channels in an electrode-cap under the 10/20 system-extended and three pairs of additional electrodes. Two pairs of electrodes, situated on the outer canthi and infra-orbital ridges, monitored eye movements; one pair was placed over the mastoids. A Common Mode Sense (CMS) active-electrode and a Driven Right Leg (DRL) passive-electrode acted as a ground during recordings. The electrodes were average-referenced offline.

2.2.5 Eye-Tracking Recordings

Eye movements were recorded using a remote Eyelink 1000 eye-tracker from SR Research with a sampling rate of 1000Hz. The eye-tracker was calibrated to each participant's dominant eye, but viewing was binocular. If participants spent over 10s before successfully fixating on the cross, a drift correction was used. After two drift corrections, a mid-block recalibration was performed. Calibration was done using a nine-point automated calibration accuracy test. Calibration was repeated if the error at any point was more than 1°, or if the average for all points was greater than 0.5°. The participants' head position was stabilized with a head and chin rest to maintain viewing position and distance constant.

2.2.6 Data Processing and Analyses

Only correctly answered trials were used for analysis. Trials in which a saccadic eye movement was recorded beyond 1.4° visual angle (70px) around the fixation location were removed from further analysis (see Fig.1 for interest areas around each fixation location). This size ensured that the areas of interest around the features were non-overlapping. This step in

the pre-processing removed an average of 2.0% (±1.7) of trials across the 20 participants included in the final sample.

The data were processed offline using the EEGLab (Derlome & Makeig, 2004) and ERPLab (http://erpinfor.org/erplab) toolboxes implemented in Matlab (Mathworks, Inc.) Average-waveform epochs of 500ms were generated (100ms pre-stimulus-onset to 400ms post-stimulus-onset) and digitally band-pass filtered (0.01–30Hz) using a two-way least-squares FIR filter. Trials containing artifacts >±70µV were then rejected (100µV was used for 6 participants). Trials were then visually inspected and those still containing artefacts were rejected. After trial rejection, participants with less than 40 trials in each condition (out of 80 initial trials) were rejected (the average number of trials per condition did not significantly differ across emotions (p = .31) or fixation location (p = .39)) (see Appendix A1 for final number of participants per condition).

Contrast and Pixel intensity[6]. To evaluate possible influences of low-level factors, I measured the mean pixel intensity and root mean squared (RMS) contrast of each picture using a home-made Matlab program and compared them across emotions using paired sample *t*-tests, with *p*-values corrected for multiple comparisons. Pixel intensity was calculated as the mean of the image's pixels intensity values and RMS contrast as the standard deviation of the pixels intensities (normalized between 0 and 1).

For each picture, the mean RMS contrast and pixel intensity were also calculated for circular areas of 1.4° visual angle around each fixation location (Fig.1) and were analyzed using a 3 (emotion) X 4 (fixation location) repeated measure analysis of variance (ANOVA).

[6] Note that the same stimuli were used in Exp.'s 1 to 3 and therefore contrast and pixel intensity values are the same in these experiments.

Behavioural Analysis. Repeated measures ANOVAs were conducted separately for percent errors and mean RTs. For each participant, only RTs within 2.5 standard deviations from the mean of each condition were kept in the mean RT calculation (Van Selst & Jolicoeur, 1994) which excluded 7.67% of the total number of trials. Within-subject factors included facial expression (3: fear, happiness, neutral) and fixation location (4: left eye, right eye, nose, mouth). Interactions were interpreted using simple main effects ANOVAs for emotion (fear, happy, neutral) conducted separately at each fixation location.

ERP Analysis. For most participants, the P1 component was maximal at electrodes O1 and O2 and was thus measured at these sites between 80 and 130ms post-stimulus-onset (peak around 100ms) using automatic peak detection. Careful inspection of the data also suggested some emotion differences on P1 at Oz so P1 was also analyzed at Oz separately. In contrast to P1, the N170 component was maximal at different electrodes across participants, and within a given participant the N170 was often maximal at different electrodes across the two hemispheres. Thus, to best capture that component, the N170 peak was measured between 120-200ms at the electrode where it was maximal for each subject and for each hemisphere (Table 1).

Table 1. *Number of subjects for whom the N170 was maximal at left (P07, CB1, P9) and right (PO8, CB2, P10, and TP10) hemisphere electrodes. LH: left hemisphere; RH: right hemisphere*

	LH		RH
P9	6	P10	8
CB1	8	CB2	5
PO7	6	PO8	5
		TP10	5
Total n	20		20

To measure the time course of the fixation and emotion effects, mean amplitudes were also calculated within six 50ms windows starting from 50ms to 350ms. Preliminary inspection of the data revealed different effects over two electrode clusters at occipital sites (O1, O2 and Oz) and at lateral-posterior sites (CB1/2, P9/10, P7/8 and PO7/8). Thus for each time window, separate analyses were conducted over these two clusters. Note that the lateral-posterior electrodes are those electrodes where the N170 was measured across participants and also included the visual P2 component (peaking around 200ms post-face onset) as well as the Early Posterior Negativity (EPN) component involved in emotion processing. P2 and EPN are broader components and best measured by mean amplitudes.

Repeated measures ANOVAs were conducted using SPSS Statistics 22. Within-subject factors included hemisphere (2: left, right), facial expression (3: fear, happiness, neutral) and fixation location (4: left eye, right eye, nose, mouth) for P1 and N170 peaks. For mean amplitude analyses, an electrode factor was added for occipital sites (3: O1, O2, Oz) and lateral-posterior sites (4: CB1/2, P9/10, P7/8, PO7/8). If necessary further analyses of the interactions found were completed with separate ANOVAs for each fixation location or each emotion. All ANOVAs used Greenhouse-Geisser adjusted degrees of freedom and pairwise comparisons used Bonferroni corrections for multiple comparisons, following the ERP data analysis guidelines (Picton et al., 2000).

2.3 Results

2.3.1 Pixel intensity (PI) and RMS contrast

Post-hoc paired *t*-tests confirmed no differences between emotions ($p > .05$ for all comparisons) for mean pixel intensity and mean contrast values (Table 2).

For mean RMS contrast in areas of 1.4° visual angle around each fixation, the highest contrast was seen for the left and right eyes (which did not significantly differ), followed by the mouth and then the nose (which did not significantly differ; effect of fixation location, $F(1.34, 9.40) = 16.34$, $p < .001$, $\eta_p^2 = .70$, all paired comparisons at *p*-values < .05; see Table 2). However, the emotion by fixation location interaction ($F(2.74, 19.18) = 11.48$, $p < .001$, $\eta_p^2 = .62$) revealed that this specific pattern was seen only for neutral faces ($F = 41.71$, $p < .001$; all significant fixation location paired comparisons at $p < .05$)[7]. For happy faces a larger contrast was seen for the mouth compared to the nose fixation ($F = 6.07$, $p < .05$). For fearful faces there was an effect of fixation location ($F = 5.22$, $p < .05$); however, pairwise comparisons were not significant. During fixation to the left eye a larger contrast was seen for neutral compared to happy faces ($F = 9.70$, $p < .01$) and larger contrast for both fearful and happy faces compared to neutral during fixation to the mouth ($F = 11.52$, $p < .01$). No emotion differences were seen during fixation to the nose ($p = .12$) and an effect of emotion was seen for fixation to the right eye ($F = 4.97$, $p < .05$); however, no significant pairwise comparisons were found following the Bonferroni corrections.

The lowest PI was seen for the left and right eyes (which did not significantly differ), followed by the mouth and the nose (which did not significantly differ; effect of fixation location,

[7] For clarity of the text, for post-hoc results only *F* and *p* values will be reported and not the degrees of freedom (as done in Neath & Itier, 2015).

$F(1.77, 12.36) = 42.29$, $p < .001$, $\eta_p^2 = .86$, all paired comparisons at p-values < .01). The emotion by fixation location interaction was also significant ($F(2.54,17.81) = 6.79$, $p < .05$, $\eta_p^2 = .49$), due to larger PI on the mouth for happy compared to fearful and neutral faces (p-values < .05). During fixation to the left eye ($p = .76$) and right eye ($p = .54$) no differences between emotions were seen. During fixation to the nose, larger PI was seen for fearful compared to happy and neutral faces ($F = 11.38$, $p < .05$) and during fixation to the mouth larger PI was seen for happy compared to fearful and neutral faces ($F = 20.99$, $p < .001$).

Table 2. *Mean pixel intensity (PI) and RMS contrast values for full faces and within 1.4° radius around the center of the left eye, right eye, nose and mouth for fearful, happy and neutral expressions used in Experiment 1 to 3 (standard errors to the means in parenthesis).*

	Mean Pixel Intensity (PI) (std. error)					Mean RMS Contrast (std. error)				
	Full Face	Left Eye	Right Eye	Nose	Mouth	**Full Face**	Left Eye	Right Eye	Nose	Mouth
Fearful	**.58 (.01)**	.43 (.02)	.44 (.04)	.52 (.02)	.49 (.03)	**.33 (.01)**	.14 (.01)	.14 (.01)	.12 (.01)	.13 (.02)
Happy	**.57 (.01)**	.44 (.03)	.44 (.03)	.51 (.02)	.55 (.02)	**.34 (.01)**	.13 (.01)	.14 (.02)	.11 (.01)	.13 (.01)
Neutral	**.57 (.01)**	.43 (.03)	.43 (.02)	.51 (.03)	.50 (.02)	**.34 (.01)**	.14 (.03)	.14 (.01)	.11 (.01)	.10 (.01)

2.3.2 Behavioural Analyses

Error rates. Participants tended to make more errors for fearful than neutral faces (main effect of emotion; $F(1.79, 34.04) = 4.76$, $p < .05$, $\eta_p^2 = .20$; fearful-neutral paired comparison at $p = .06$; see Table 3). Additionally, fewer errors were made during fixation on the nose compared to fixation on the left and right eye (main effect of fixation location; $F(2.31, 43.89) = 3.58$, $p < .05$, $\eta_p^2 = .16$; paired comparisons significant at $p < .05$). No differences were seen for miss rates.

Response times (RTs). Responses were slowest for fearful expressions (main effect of emotion, $F(1.71, 32.41) = 21.57$, $p < .001$, $\eta_p^2 = .53$; fearful-neutral and fearful-happy paired comparisons significant at $p < .001$; Table 3) and faster for nose fixation (main effect of fixation location, $F(2.62, 49.77) = 7.42$, $p < .01$, $\eta_p^2 = .28$; significantly faster for the nose than the mouth and right eye, $p < .05$). No other effects were seen.

Table 3. *Mean (A) percent error, (B) reaction time (RT) and (C) misses/no-response values for fearful, happy and neutral expressions presented during the gender discrimination task (standard errors to the means in parenthesis).*

	Mean Error (%) (std. error)	Mean Reaction Time (RT) (ms) (std. error)	Mean Misses (%) (std. error)
Fearful	9.7 (1.0)	629.54 (12.61)	9.3 (0.9)
Happy	8.1 (1.0)	619.94 (12.45)	9.1 (0.9)
Neutral	7.6 (0.9)	614.86 (12.51)	9.6 (0.9)

2.3.3 ERP Analyses

2.3.3.1 Effects of fixation location and emotion at occipital sites (O1, O2, Oz).

P1 Peak Amplitude. At O1/O2, P1 amplitude was overall largest for fixation to the mouth (main effect of fixation, $F(2.73, 51.92) = 11.19$, $p < .001$, $\eta_p^2 = .37$) (see Fig. 3A). An interaction between fixation location and hemisphere was also found ($F(2.19, 41.56) = 18.96$, $p < .001$, $\eta_p^2 = .50$) due to eye fixations yielding opposite effects. On the left hemisphere, P1 was larger for the mouth and left eye (which did not differ significantly) compared to the right eye and the nose fixations (which did not differ) ($F = 11.22$, $p < .001$). On the right hemisphere, P1 was larger for the mouth and right eye (which did not differ significantly) compared to the left eye and nose fixations which did not differ ($F = 15.83$, $p < .001$; significant paired comparisons right eye-left

eye/nose $p < .05$, mouth-left eye/nose $p < .001$). No effects of emotion or emotion by fixation location interaction were seen (Fig. 3B).

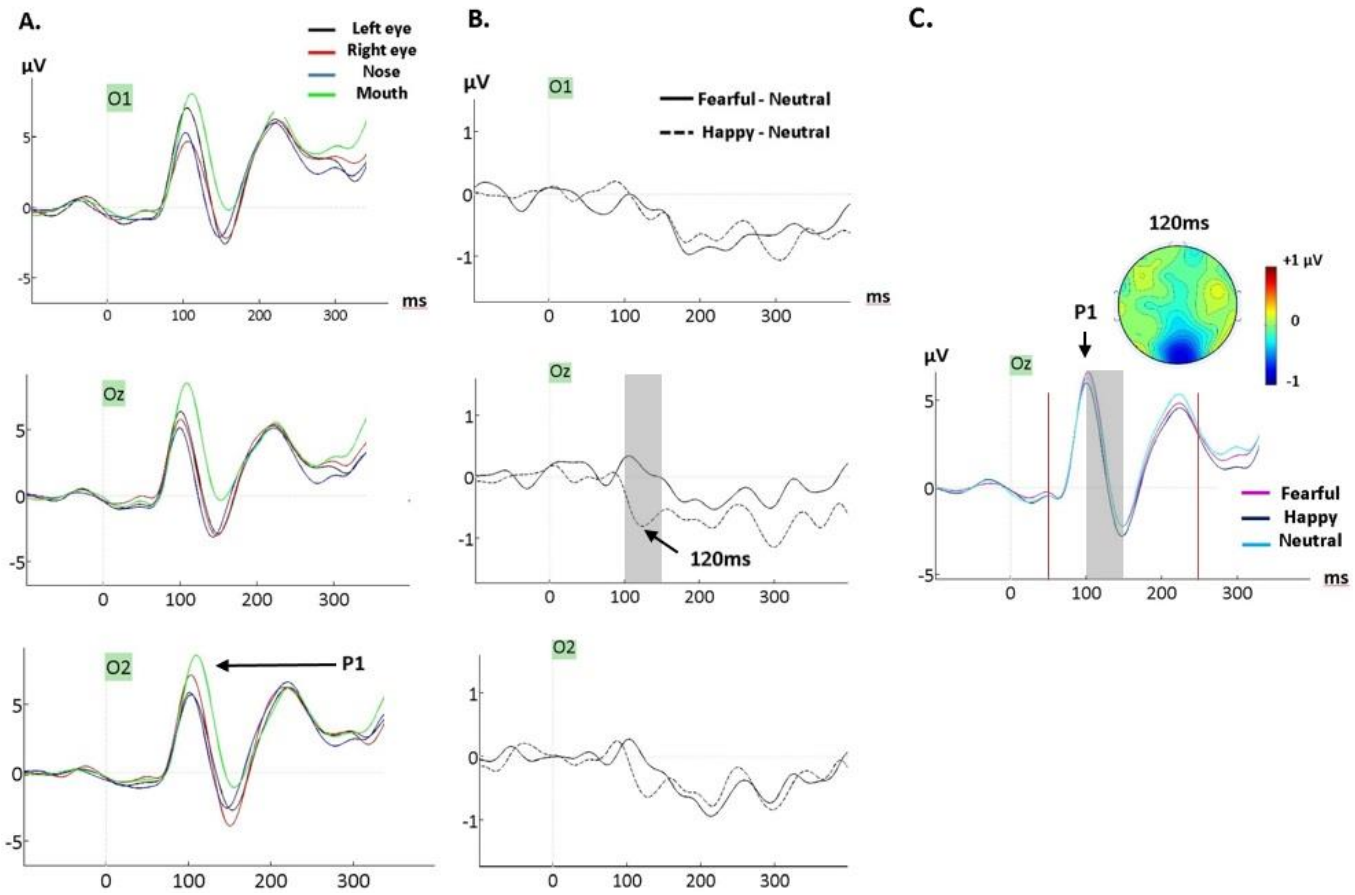


Figure 3. Effects of Fixation Location and Emotion at Occipital sites (Exp.1)

(A) Grand-averages (across the participant group) featuring the P1 component for neutral faces at O1, O2, and Oz electrodes, showing effects of fixation locations with larger amplitudes for mouth fixation and opposite hemispheric effects for eye fixations. (B) Grand-average difference waveforms generated by subtracting ERPs to neutral from ERPs to fearful faces (F-N, solid line) and ERPs to neutral from ERPs to happy faces (H-N, dashed line) at O1, O2 and Oz. A clear difference peak for happy-neutral was seen between 100 and 150ms at Oz and O2 (gray band, peak of the effect around 120ms) and was confirmed by mean amplitude analysis at occipital sites during that time window (see main text and Table 4). (C) Grand-averaged waveforms for fearful, happy and neutral faces (across fixation locations) at Oz. The early effect of emotion for happy faces started on the P1 peak at Oz. The gray interval (100-150ms) is where the effect emerged, peaking at 120ms. The red vertical lines represent the limits of the period during which mean amplitudes were analyzed (50-350ms).The topographic map shows the voltage distribution of the H-N amplitude difference at 120ms where the “happy effect” was maximal at medial occipital site.

P1 at Oz was also larger for fixation to the mouth compared to the left eye, right eye and nose which did not differ significantly from each other (main effect of fixation location, $F(2.66, 50.44) = 10.43$, $p < .001$, $\eta_p^2 = .35$; significant paired comparisons with mouth fixation at $p < .05$) (Fig. 3A). However, in contrast to O1 and O2, an effect of emotion was found on P1 at Oz due to a reduced positivity for happy compared to fearful and neutral expressions (main effect of emotion, $F(1.74, 33.13) = 6.68$, $p < .01$, $\eta_p^2 = .26$; significant happy-fearful paired comparison $p < .05$, happy-neutral paired comparison $p = .06$) (see Fig 3C). Difference waveforms (fear-neutral and happy-neutral) confirmed this localized effect of emotion at medial occipital site and revealed that this "happy effect" was in fact largest around 120ms (Fig. 3B and 3C map), i.e., after the P1. This effect was confirmed with mean amplitude analyzes during the 100-150ms window (see below). For the remainder of the thesis, the "happy effect" will denote significantly smaller amplitudes for happy than neutral faces, and the "fearful effect" will denote significantly smaller amplitudes for fearful than neutral faces.

Mean Amplitudes over Six Time Windows (O1, O2, Oz). Statistical results for these analyses (50-350ms) are reported in Table 4 and visually depicted in Figures 3 and 4.

Between 50 and 100ms, fixation to one eye yielded opposite effects between the two hemispheres, with larger amplitudes for left eye fixation than right eye fixation on the left hemisphere and vice versa for the right hemisphere (Electrode by fixation location interaction, Table 4). These effects of fixation were virtually identical to those seen on P1 peak (analyzed at O1/O2) and disappeared by 150ms. Larger amplitudes for fixation to the mouth was seen as a main effect of fixation between 50 and 150ms. This effect re-appeared more weakly between

250 and 350ms, with larger amplitudes for mouth fixation significant during the last time window (Table 4, Fig. 3A).

An emotion effect was first seen during the 100-150ms time window with smaller amplitudes for happy compared to neutral (and fearful) expressions (Table 4, Fig. 3C). An electrode by emotion interaction revealed this effect was only seen at O2 and Oz electrodes. This effect of emotion mirrors that found on the P1 peak at Oz reported previously. During the 150-200ms interval smaller amplitudes were seen for both fearful and happy compared to neutral expressions but only for the mouth fixation condition (emotion by fixation location interaction, Table 4). Between 200 and 300ms, both fearful and happy expressions elicited smaller amplitudes compared to neutral expressions regardless of fixation location. During the 300-350ms window this effect of emotion was significant for happy faces only (happy-neutral comparison p =.003; happy-fearful p =.067).

Thus, happy faces elicited smaller amplitudes than neutral faces at occipital sites from 100 until 350ms, as clearly seen on the difference waveforms and their topographic maps (Fig. 4, see also Fig. 3B). In contrast, fearful faces elicited smaller amplitudes than neutral faces a bit later, starting at 150ms and vanishing by 300ms. Figure 4 also suggests that the effect for fear was mostly lateral (as discussed next) and only weakly occipital, while the opposite was found for happy faces.

Table 4. *Exp. 1 (GD task) statistical effects on mean amplitudes analyzed over six 50ms time windows at occipital sites (O1, Oz, O2), with F, p and η_p^2 values. LH, left hemisphere; RH, right hemisphere; LE, left eye; RE, right eye; No, nose; Mo, mouth; F, fear; H, happy; N, neutral. Main effects p values: p* < .05; p** < .01; p*** < .001; p**** < .0001; ns, not significant. Bonferroni-corrected paired comparison tests are also reported (e.g., H < F + N means that the main effect of emotion is due to significantly smaller mean amplitude for happy compared to both fearful and neutral expressions while H + F < N means that both happy and fearful faces elicited significantly smaller amplitudes than neutral faces).*

Main effects and interactions	50-100ms	100- 150ms	150- 200ms	200-250ms	250-300ms	300-350ms
Electrode	-	F = 6.50, p* , η_p^2 = .26 O1 + O2 > Oz	-	F = 3.73, p* , η_p^2 = .16 O1 + O2 > Oz	F = 5.31, p*, η_p^2 = .22 O1 + O2 > Oz	-
Fixation location	F= 11.23, p***, η_p^2 = .37 Mo > all	F = 25.37, p****, η_p^2 = .57 Mo > all	-	. -	F = 3.57, p*, η_p^2 = .16 (Mo + LE+) RE > No	F = 5.03, p**, η_p^2 = .21 Mo > No
Emotion	-	F = 11.51, p***, η_p^2 = .38 H < F + N	F = 8.55, p**, η_p^2 = .31 H + F < N	F = 7.87, p**, η_p^2 = .29 H + F < N	F = 6.97, p**, η_p^2 = .27 H + F < N	F = 9.29, p**, η_p^2 = .33 H < F + N
Electrode X Fixation location	F= 16.05, p****, η_p^2 = .46 • O1: F = 11.22, p****, η_p^2 = .37 Mo + LE > RE + No • O2: F = 15.83, p****, η_p^2 = .46 Mo + RE > LE + No • Oz: F = 10.43, p****, η_p^2 = .35 Mo > all	F = 4.2, p**, η_p^2 = .18 • O1: F = 13.28, p****, η_p^2 = .41 Mo + LE > RE + No • O2: F =25.21, p****, η_p^2 = .57 Mo > all • Oz: F = 28.47, p****, η_p^2 = .60 Mo > all	-	-	-	F= 4.03, p**, η_p^2 = .18 • O1: F = 7.51, p**, η_p^2 = .28 Mo > LE + No • O2: No effect • Oz: F = 6.35, p**, η_p^2 = .25 Mo > No
Electrode X Emotion	-	F = 3.70, p*, η_p^2 = .16 • O1: No effect • O2: F = 5.77, p**, η_p^2 =.23 H < N + F • Oz: F = 18.35, p****, η_p^2 = .49 H < N + F	-	-	-	-
Emotion X Fixation location	-	-	F= 3.03, p*, η_p^2 = .14 • Mo: F = 22.58, p****, η_p^2 = .54 H + F < N • LE: no effect • RE: no effect • No: no effect	-	-	-

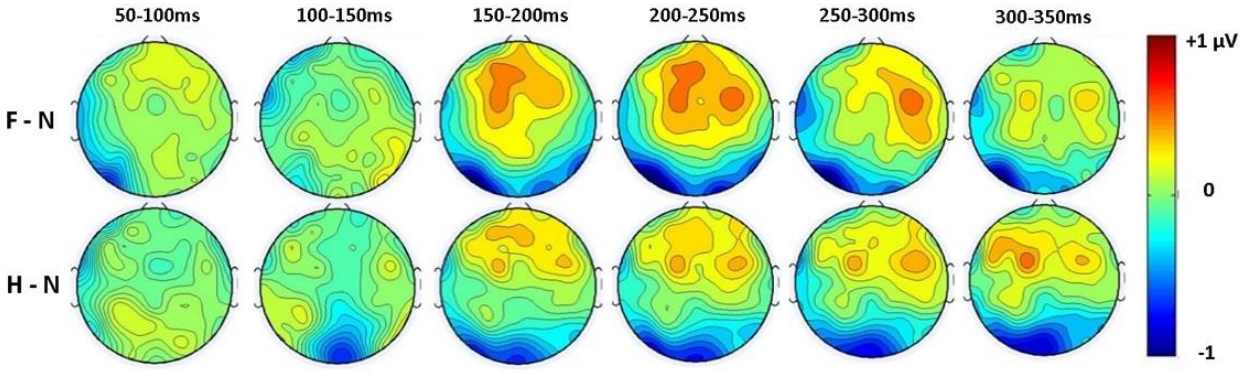


Figure 4. 2D Topographical Maps of Fearful-Neutral and Happy-Neutral Voltage Differences (Exp.1)

Mean voltage distribution maps of the grand-average difference waveforms between fear and neutral (F-N) and happy and neutral faces (H-N) across six 50ms time intervals from 50ms to 350ms (averaged across fixation location).

2.3.3.2 Effects of fixation location and emotion at lateral-posterior sites (CB1/2, P9/10, P7/8, PO7/8)

N170 Peak Amplitude. The N170 amplitude was larger for fixation to the left and right eye (which did not differ) compared to fixation to the mouth and nose which did not differ significantly (main effect of fixation location, $F(2.46, 46.80) = 16.43$, $p < .0001$, $\eta_p^2 = .46$; all paired comparisons at p-values < .01) (Fig. 5A). No other significant effects were seen and in particular there was no main effect of emotion, or any interactions involving emotion.

P1-to-N170 amplitude. As effects of fixation location were found for P1 at occipital sites, I performed peak-to-peak analyses to track possible influences of P1 onto N170 measures at these lateral sites. I took the amplitude differences between the P1 and N170 at the electrode at which the N170 was largest for each hemisphere and each subject[8]. Amplitude differences were

[8] Note that the P1 had to be re-measured at these lateral-posterior sites for this analysis

larger in the right compared to the left hemisphere (main effect of hemisphere, $F(1, 19) = 5.14$, $p < .05$, $\eta_p^2 = 21$; significant paired comparison $p < .05$) and were larger during fixation to both the left and right eyes (which did not differ) compared to the nose and mouth (which did not differ) (main effect of fixation location, $F(1.79, 34.07) = 32.27$, $p < .001$, $\eta_p^2 = .63$; significant left eye-nose/mouth and right eye-nose/mouth paired comparisons $p < .001$). This confirmed the fixation location found for the N170 peak. In addition however, an interaction between fixation location and hemisphere was seen ($F(2.64, 50.22) = 16.42$, $p < .0001$, $\eta_p^2 = .46$), due to opposite effects of eye fixation in each hemisphere, driven by the P1 (Fig. 5A). On the left hemisphere, the main effect of fixation location ($F(2.43, 46.27) = 19.4$, $p < .0001$, $\eta_p^2 = .51$) was due to larger amplitude differences for the left eye compared to all other fixation locations (amplitude for the right eye was also larger than for the mouth). On the right hemisphere, the fixation location effect ($F(1.87, 35.67) = 34.31$, $p < .0001$, $\eta_p^2 = .64$) was due to amplitudes being larger for both eye fixations (which did not differ) compared to both nose and mouth (which did not differ).

Interestingly, in contrast to the lack of emotion effect for N170 peak, there were significant interactions between hemisphere and emotion ($F(1.91, 36.29) = 4.54$, $p = .019$, $\eta_p^2 = .19$) and hemisphere, emotion and fixation location ($F(4.81, 91.31) = 2.96$, $p = .017$, $\eta_p^2 = .14$). On the left hemisphere, an emotion by fixation location interaction ($F(4.20, 79.71) = 3.15$, $p = .017$, $\eta_p^2 = .14$) was due to a larger P1-N170 amplitude difference for happy faces compared to neutral and fearful faces (significant paired comparisons $p < .01$) that was seen only when fixation was on the mouth (mouth: effect of emotion, $F = 10.10$, $p < .001$; significant paired comparisons $p < .01$). There was no effect of emotion when fixation was on the left eye ($p = .27$), right eye ($p = .54$) or nose ($p = .24$). On the right hemisphere, the P1-N170 amplitude difference was larger for

happy compared to neutral expressions regardless of fixation location (main effect of emotion, $F(1.85, 35.44) = 4.59$, $p = .019$, $\eta_p^2 = .20$; significant happy-neutral paired comparison $p < .05$, fear-neutral paired comparison borderline at $p = .053$).

Overall, taking P1 into account (by calculating P1 to N170 peak differences) revealed interactions between fixation and hemisphere as seen for P1 peak, as well as emotion effects not seen on either the P1 (at O1/O2 sites) or the N170 peaks.

Mean Amplitude analyses over Six Time Windows (CB1/2, P7/8, P9/10, PO7/8). Statistical results for these analyses (50-350ms) are reported in Table 5 and visually depicted in Figures 4, 5 and 6.

A hemisphere by fixation location interaction was seen between 50ms and 100ms (Table 5), due to fixation to the eyes yielding opposite effects on each hemisphere, with larger amplitude for fixation to the left eye compared to the right eye on the left hemisphere and vice versa for the right hemisphere. At 100-150ms, this fixation by hemisphere interaction became stronger, with larger amplitude for the left eye fixation compared to all other fixations on the left hemisphere, and larger amplitude for the right eye than the other fixations on the right hemisphere. These effects between 50 and 150ms were driven by the P1 as clearly seen on Fig.5A, and as also found in the P1-N170 amplitude difference analysis. Between 150 and 200ms, in line with the fixation effect seen for N170, the mean amplitudes were larger for both the left and the right eye fixations (which did not differ significantly) compared to both the nose and mouth fixations (which did not differ significantly), an effect that was most pronounced at P9/P10 and CB1/CB2 sites. No effect of fixation location was seen after 200ms.

Table 5. *Exp. 1 (GD task) statistical effects on mean amplitudes analyzed over six 50ms time windows at lateral-posterior sites (CB1/2, P7/8, PO7/8, P9/10), with F, p and η_p^2 values. LH, left hemisphere; RH, right hemisphere; LE, left eye; RE, right eye; No, nose; Mo, mouth; F, fear; H, happy; N, neutral. Main effects p values: p* < .05; p** < .01; p*** < .001; p**** < .0001; ns, not significant. Bonferroni-corrected paired comparison tests are also reported (e.g., F < H + N means that the main effect of emotion is due to significantly smaller mean amplitude for fearful compared to both happy and neutral expressions while F + H < N means that amplitudes were significantly smaller for both fearful and happy faces compared to neutral faces).*

Main effects and interactions	50-100ms	100- 150ms	150- 200ms	200-250ms	250-300ms	300-350ms
Electrode	*F* = 4.91, *p** , η_p^2 = .21 PO7/8 < P9/10 < CB1/2 < P7/8	*F* = 16.10, *p**** , η_p^2 = .46 P9/10 < CB1/2 < P7/8 < PO7/8	*F* = 21.27, *p**** , η_p^2 = .53 P9/10 < CB1/2 + P7/8 < PO7/8	*F* = 61.83, *p****, η_p^2 = .77 P9/10 < CB1/2 < P7/8 < PO7/8	*F* = 53.27, *p**** , η_p^2 = .74 P9/10 < CB1/2 < P7/8 < PO7/8	*F* = 47.69, *p**** , η_p^2 = .72 P9/10 < CB1/2 < P7/8 < PO7/8
Hemisphere	-	-	-	*F* = 5.72, *p**, η_p^2 = .23 LH < RH	-	*F* = 14.52, *p**, η_p^2 = .43 LH < RH
Fixation location	-	*F* = 14.97, *p****, η_p^2 = .44 No < all	*F* = 14.18, *p****, η_p^2 = .43 LE + RE < No + Mo	-	-	-
Emotion	-	-	*F* = 13.87, *p****, η_p^2 = .42 F < H + N	*F* = 23.79, *p****, η_p^2 = .56 F < H < N	*F* = 5.88, *p**, η_p^2 = .24 F < N	*F* = 5.50, *p**, η_p^2 = .23 H < N
Electrode X Fixation location	-	*F* = 9.46, *p****, η_p^2 = .33 • CB: *F* = 11.04, *p****, η_p^2 = .38 No < all • P7/8: *F* = 12.01, *p****, η_p^2 = .39 No < all • P9/10: *F* = 16.53, *p****, η_p^2 = .47 No < M < LE + RE • PO7/8: *F* = 13.46, *p****, η_p^2 = .42 No < LE+RE < M	*F* = 5.32, *p***, η_p^2 = .22 • CB: *F* = 16.64, *p***, η_p^2 = 47 LE+RE < No + Mo • P7/8: *F* = 3.59, *p**, η_p^2 = .16 No sign. paired comp • P9/10: *F* = 15.94 *p***, η_p^2 = .46 LE + RE < No + Mo • PO7/8: *F* = 5.67 *p***, η_p^2 = .23 LE (+RE) < No (+ Mo)	-	-	-
Hemisphere X Fixation location	*F* = 9.38, *p***, η_p^2 = .33 • LH: *F* = 5.57, *p***, η_p^2 = .23 LE > RE • RH: *F* = 3.49, *p**, η_p^2 = .16 RE > LE (*p*=.082)	*F* = 11.91, *p****, η_p^2 = .39 • LH: : *F* = 11.64, *p****, η_p^2 = .38 LE > all • RH: *F* = 14.96, *p****, η_p^2 = .44 RE > all	-	-	-	-
Hemisphere X Emotion	-	-	-	-	*F* = 4.14, *p**, η_p^2 = .18 • LH: *F* = 11.45, *p****, η_p^2 = .38 F < H + N • RH: ns	*F* = 3.61, *p**, η_p^2 = .16 • LH: *F* = 7.72, *p***, η_p^2 = .29 F + H < N • RH: ns
Electrode X Hemisphere X Emotion	*F* =3.23, *p**, η_p^2 = .15 • PO7: *F* = 12.38, *p****, η_p^2 = .39; F < H + N • P7: *F* = 8.44, *p***, η_p^2 = .31; F < H + N	-	-	-	-	-

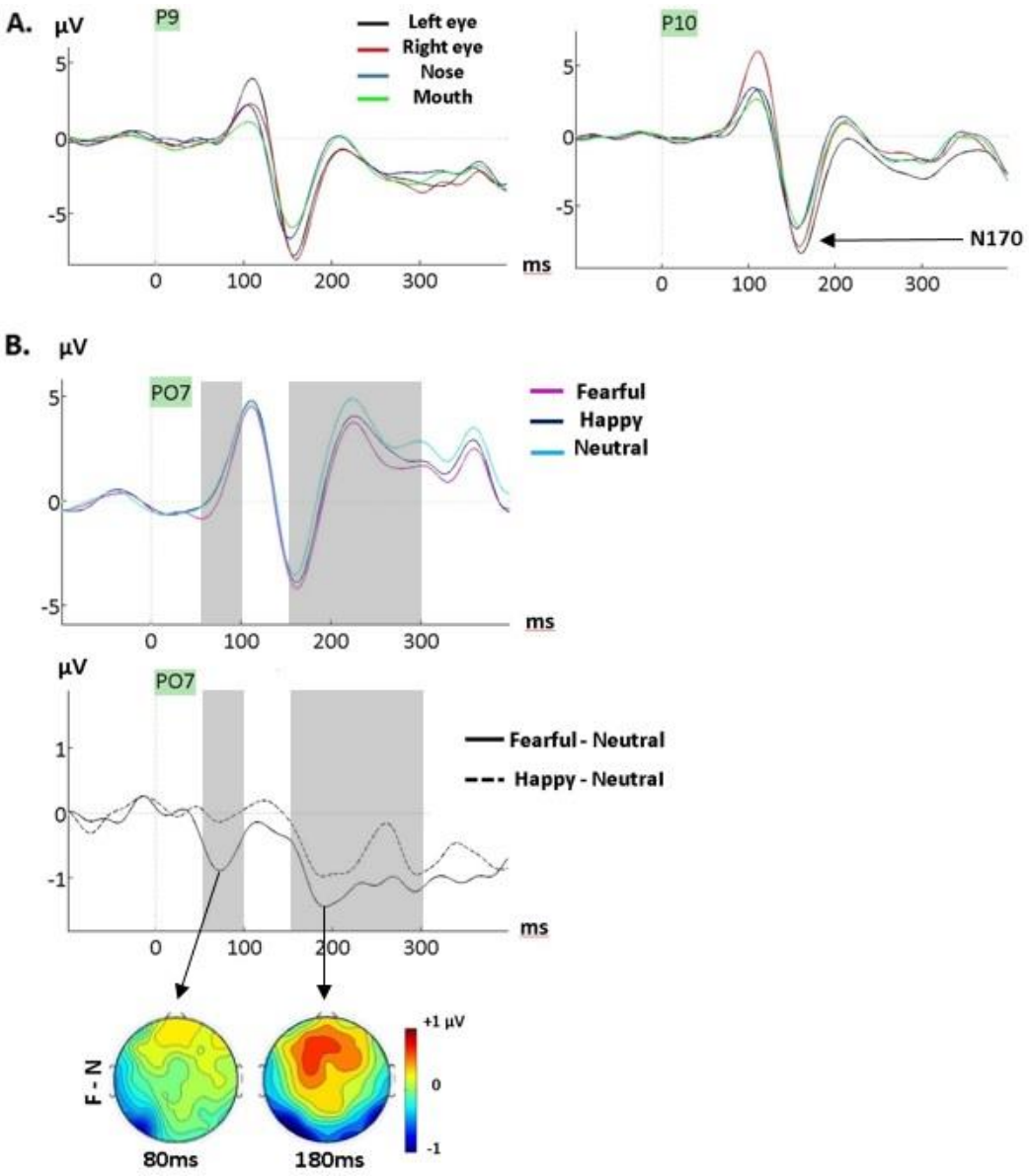


Figure 5. Effects of Fixation Location and Emotion at Lateral-Posterior Sites (Exp.1)

(A) Grand-averages featuring the N170 component for neutral faces at P9 and P10 as a function of fixation location clearly showing larger amplitudes for eyes than nose and mouth fixation. (B) The early and later effect of emotion for fearful faces at temporal-parietal sites. *Top:* Grand-average for fearful, happy and neutral faces (across fixation locations) at PO7 site where the early fearful effect was maximal. *Bottom:* Grand-average difference waveforms generated by subtracting ERPs to neutral from ERPs to fearful faces (F-N, solid line) and ERPs to neutral from ERPs to happy faces (H-N, dashed line) at PO7. The gray intervals (50-100ms) and (150-300ms) are where the early and later emotion effects for fear were seen. The maps show the voltage difference between fearful and neutral faces (F-N) across the scalp at the latency at which the early (80ms) and later (180ms) effects were largest.

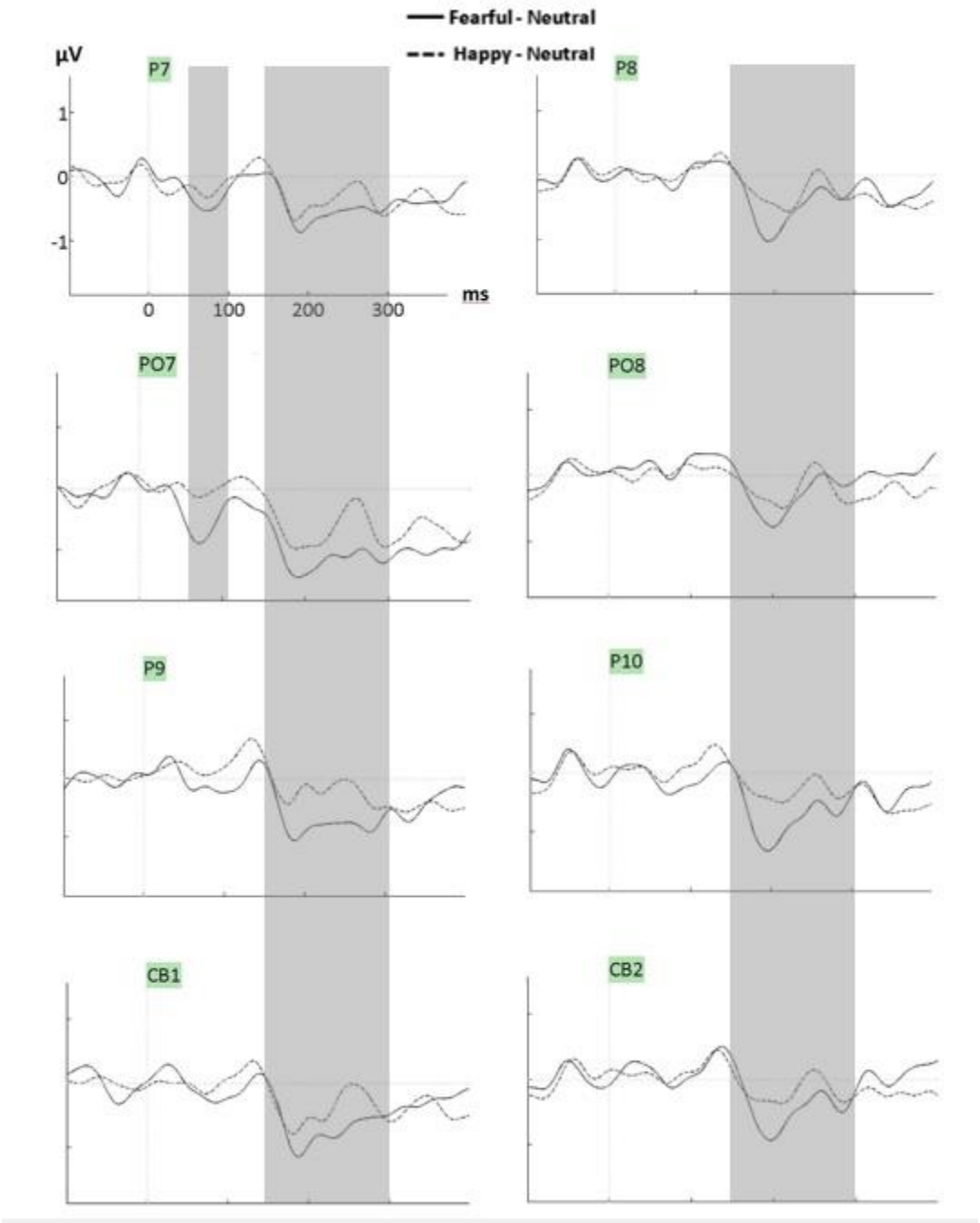


Figure 6. Fearful-Neutral and Happy-Neutral Difference Waves at Lateral-Posterior Sites (Exp.1)

Grand-average difference waveforms generated by subtracting neutral from fearful and happy conditions (F-N and H-N, averaged across fixation locations) at lateral-posterior sites (CB1/2, P7/8, PO7/8, P9/10). The gray zones highlight the time windows during which the effect for fear was significant, an early effect restricted to P7 and PO7 electrodes during 50-100ms and a later effect at all lateral-posterior sites (150-300ms).

A very early effect of emotion was seen between 50 and 100ms that was restricted to PO7 and P7 (left hemisphere) electrodes (electrode by hemisphere by emotion interaction, Table 5), with smaller amplitude for fearful faces compared to neutral (and happy) faces (Fig. 5B). This effect peaked at ~80ms. This fearful effect appeared again later beginning at 150ms and lasted until 300ms, this time at all lateral-posterior sites (Fig. 5B, Fig.6). During that time, amplitudes for fearful faces were smaller than amplitudes for both neutral and happy faces, with the fearful-neutral difference peaking around 180ms (Fig. 5B). Mean amplitudes for happy faces were also significantly smaller than for neutral faces between 200-250ms and again later between 300 and 350ms (Fig.6). Interestingly, between 250 and 350ms the emotion effects were seen only for the left hemisphere (P7, PO7, CB1 and P9; hemisphere by emotion interaction, Table 5), as clearly seen on Fig.4.

2.4 Discussion

The aim of the present gender categorization task was to test the effect of fixation to specific facial features on the neural response to facial expressions between 50 and 350ms (encompassing the P1, N170 and Early Posterior Negativity -EPN). Also tested was the idea that fixation to fearful eyes might be driving the debated N170 modulation by emotion. Using eye-tracking to enforce correct fixation to facial features, analyses revealed that the P1 and N170 peaks were sensitive to fixation location but not to emotion. Emotion effects, however, were seen at posterior sites, mostly medially and occipitally for happy expressions, and mostly laterally for fearful expressions.

2.4.1 Fixation location and facial emotion influenced gender discrimination

Behavioural performance was impacted by fixation location, with fewer errors and shorter RTs when fixation was on the nose compared to other fixated locations. This result is in line with the idea that when the whole face is available, gender discrimination requires holistic processing (Brown & Perrett, 1993; Zhao & Hayward, 2010) which is most efficient around the face center, situated close to the nose (e.g., Bindemann, Scheepers, & Burton, 2009; de Heering et al., 2008). Note that this does not undermine the idea that some face parts might convey face gender better than others when presented in isolation, as recently reported (Best, Minshew, & Strauss, 2010). Most importantly, despite the task being emotion-irrelevant, emotion impacted behavioural performance as seen by participants' trend toward larger error rates for fearful compared to neutral faces and significantly longer RTs for fearful faces compared to both happy and neutral faces. Similar results have been reported by Scheller, Büchel, & Gamer (2012) with lower hit rates for fearful and neutral than happy faces in a gender categorization task where faces were presented for 2 seconds. This finding is sensible given face gender discrimination requires virtually no attention (Reddy, Wilken. & Koch, 2004), leaving attention resources available to process the emotions as demonstrated here. Facial expression categories were processed during the present emotion-irrelevant task and impacted the efficiency of gender discrimination.

2.4.2 Different sensitivity to fixation location for P1 and N170

The P1 component is sensitive to low-level stimuli characteristics such as contrast, luminance, color and spatial frequencies (Rossion and Jacques, 2008). Research controlling for stimuli low-level differences have demonstrated that the P1 does not differ between object

categories while the following face-sensitive N170 does. Thus these components reflect distinct stages of visual processing with only the N170 reflecting high level vision and face categorization (e.g., Ganis et al., 2012; Jemel et al., 2003; Rossion & Caharel, 2011; Tarkiainen, Cornelissen, & Salmelin, 2002).

As predicted, a clear fixation effect was seen with larger P1 amplitude for the right than for the left eye on the right hemisphere and vice versa for the left hemisphere. This effect was seen as early as 50-100ms at occipital sites (Fig.3A) and between 50 and 150ms at lateral-posterior sites (Fig.5A). This fixation effect was also found on the P1-to-N170 analysis which was driven by the P1. This effect of fixation reflected hemifield presentation effects given the fact that most of the facial information was in the left visual field when fixation was on the right eye and in the right visual field when fixation was on the left eye (Fig.1). This hemifield effect was also reported in three recent studies using similar gaze-contingent presentations (de Lissa et al., 2014; Nemrodov et al., 2014; Zerouali et al., 2013).

In addition, at occipital sites, a delayed and larger P1 response was seen when fixation was on the mouth compared to each of the other locations. This effect was seen during the entire epoch (although not significantly between 150 and 300ms, Fig.3A, Table 4) and likely reflected sensitivity to the position of the face on the screen. Most of the facial information is in the upper visual field when fixation falls on the mouth compared to the eyes or the nose. The P1 has been shown to vary with ipsi/contra-lateral presentations of simple checkerboards presented in the four visual field quadrants but does not vary between the upper and lower visual fields (Clark, Fan, & Hillyard, 1995; Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002, p101). One possibility

is that the visual system is more sensitive to the upper visual field for meaningful stimuli such as faces which are viewed most often in that area.

As also predicted, I replicated the finding by Nemrodov et al. (2014) of larger N170 amplitude for fixation on the left and right eyes (which did not differ significantly) compared to the nose and the mouth which also did not differ significantly (see also de Lissa et al., 2014). This effect is not attributable to a simple face position effect as seen for the P1. The N170 amplitude has been shown to decrease with face eccentricity (Rousselet, Husk, Bennett, & Sekuler, 2005); therefore, if this N170 amplitude modulation reflected a face position effect we would expect to see smaller, rather than larger, N170 amplitude for fixation to the eyes, given the more lateral position of the face for these fixation locations compared to the midline fixation locations (nose and mouth). Further demonstration that this N170 modulation reflects a true eye sensitivity was provided by Nemrodov et al. (2014) who showed that the same eye fixation locations did not yield these larger N170 amplitudes when the eyes were not present in fovea (in eyeless faces), despite the same positions of those faces on the screen. This sensitivity of the N170 component to eyes has been shown using isolated eye stimuli, with larger N170s to isolated eyes than full faces (e.g., Bentin et al., 1996; Itier et al., 2006, 2007, 2011) that is seen as early as four years of age (Taylor, Edmonds, McCarthy, & Allison, 2001). The N170 sensitivity to eyes has also been shown using the response classification technique *Bubbles*, which reveals portions of the face, in gender and emotion discrimination tasks (e.g., Rousselet et al., 2014; Schyns et al., 2003, 2007 2009). The eye sensitivity *within* full faces as shown here provides further support to the hypothesis of an eye detector during the processing of the face structure (Nemrodov et al., 2014).

The current study demonstrates that this eye sensitivity is also seen to the same extent for faces expressing fear and happiness and is thus largely facial expression invariant.

In contrast to the P1 and N170 components, there was no effect of fixation location after 200ms at lateral-posterior sites (where P2 and EPN were seen), as also predicted. This result is in line with the idea that the eye sensitivity is specific to the face structural encoding stage as indexed by the N170.

2.4.3 Early and later occipital effects for happy facial expressions

Using stimuli that did not significantly differ in overall mean pixel intensity and contrast, an early happy effect was seen at medial occipital site Oz that began around 100ms and peaked around 120ms, i.e., *between* P1 and N170 peaks. After 150ms this effect was seen more broadly including lateral-occipital sites O1 and O2 and was sustained until 350ms. This effect was seen as a negative amplitude difference at occipital sites (happy-neutral difference waves) along with a positive counterpart at frontal sites on topographic maps (Fig.3-4). The effect spread a little to the posterior lateral sites between 200-250ms and 300-350ms (Table 5), with a seemingly left-dominant distribution (Fig.4, hemisphere interaction only between 300 and 350ms). The P1-N170 analysis at lateral sites also revealed a difference between happy and neutral expressions which was seen regardless of fixation location on the right hemisphere but was seen only for fixation on the mouth on the left hemisphere. The only other time window during which emotion interacted with fixation location was between 150 and 200ms at occipital sites (Table 4), with again a difference between happy and neutral expressions seen only for the mouth fixation. Although the present happy-neutral difference started on P1, it was maximal *after* P1, around

120ms, and no such effect was seen for fearful faces, suggesting that this effect was specific to the processing of happy expressions.

Few studies have focused on the ERPs in response to happy faces and this occipital distribution is not often reported. The few studies that have found effects of facial expression on the P1 have reported larger P1 for fearful than neutral or happy faces (see Vuilleumier and Pourtois, 2007 for review) but typically no difference between happy and neutral faces. However, the present data suggest a very localized happy effect at midline site for P1, rather than at the classic lateral sites (including O1/O2), which might have been missed by most previous studies. In an explicit emotion categorization task, Morel et al. (2014) recently reported an early happy effect with a larger P1 for happy than neutral faces (i.e., the opposite as found here) in the right hemisphere, but this was seen only for highly anxious participants and was thus likely the result of attentional demands, rather than emotional effects *per se*. In non-anxious participants, no emotion difference was seen on the lateral P1 (similar to our non-anxious sample); medial occipital sites were not analyzed. During a face-decision task (categorizing faces as intact or smeared) Schacht and Sommer (2009) reported an enhanced negativity for happy compared to neutral (and angry) faces between 128-144ms at parieto-occipital sites. Their topographic map resembles the present occipital distribution although also included parietal areas. Midline sites were not measured in that study. Let's note that although the present happy-neutral difference started on P1, it was maximal *after* P1, around 120ms, and no such effect was seen for fearful faces, which makes it unlikely a general emotional effect or a simple attentional effect. The data suggest that this effect was specific to the processing of happy expressions.

The present occipital effect for happy faces echoes results reported by Halgren et al. (2000) who recorded magnetic fields in response to various stimuli including happy and sad faces while participants identified repeated faces. Results indicated a midline occipital source in or near the calcarine fissure (around areas V1-V2) that discriminated happy from neutral expressions between 100-120ms post-stimulus. That source was separate from the more lateral and later source that corresponded to the magnetic equivalent of the N170, and was also sensitive to more sensory aspects of the stimuli. Halgren et al. (2000) proposed that a fast discrimination of diagnostic cues such as the smile, based on luminance and contrast, could occur within 100-120ms in those early visual areas and then be relayed rapidly to the amygdala by direct V2-amygdala connections. This explanation is possible here given the local pixel and contrast differences between emotions seen for the mouth area of our stimuli.

The current findings however, further suggest that this occipital activity is seen all the way until at least 350ms. From 150-350ms, it was accompanied by more temporal negativities as well as frontal positivities, which suggests changes of the underlying generators with time. Overall this "happy effect" appears to recruit different spatio-temporal networks with distinctive scalp distributions than the commonly reported rapid processing of fearful faces discussed below.

2.4.4 Early and later lateral-posterior effects for fearful expressions

Early effects of fearful faces have been debated. Most studies have reported no modulation of the P1 by emotion (Palermo and Rhodes, 2007; Vuilleumier and Pourtois, 2007); however, a few have reported enhanced P1 for fearful compared to neutral faces in gender discrimination tasks (Pourtois et al., 2005; Wijers et al., 2012), oddball detection tasks (Batty and Taylor, 2003), and passive viewing of emotional faces (Smith et al., 2013). The current results

however, suggest modulations by fearful expression *before* the P1 and only for fearful faces; no effect of fear was seen on the P1 itself, at lateral or medial occipital sites. This early effect of fearful expressions was localized to the left hemisphere seen clearly at PO7 and to a lesser extent at P7 during the 50-100ms time window, peaking around 80ms (Fig.4-6). It is unclear what this very early modulation represents and it will have to be reproduced before any conclusion can be drawn.

After this very early effect, modulations of ERPs by fearful faces were next seen right after the N170 component and all the way until 300ms (Table 5, Fig.4-6). The effect of facial emotions on the N170 has been debated with several studies reporting no modulation by emotion (see reviews by Eimer & Holmes, 2007 and see Rellecke et al., 2013) while others did report increased N170 with fearful faces (e.g., Batty and Taylor, 2003; Blau et al., 2007; Leppänen et al., 2008). However, previous studies have not controlled gaze fixation on the features of facial emotional stimuli. This is important given recent reports of spontaneous saccades toward the eyes of fearful expressions even with stimuli presented for only 150ms (Gamer et al., 2013). I hypothesized that the early ERP modulations of the N170 by fearful faces previously reported might have been driven by attention to the eyes. I reasoned that if this was the case, then early ERP responses would be larger for fearful than happy or neutral faces when fixation was on the eyes but not when fixation was on the nose or mouth. The present results revealed no modulation of the N170 peak amplitude by emotional faces and no interaction of emotion with fixation location. This result is in line with the lack of modulation of the N170 by emotion reported in previous gender discrimination tasks (Pourtois et al., 2005; Sato et al., 2001; Wijers & Banis, 2012). The lack of emotion by fixation interaction on the N170 suggests that the eye sensitivity demonstrated by

this component is largely independent of facial expression of emotion, as mentioned earlier. Attention to the eyes is thus unlikely the reason why previous studies reported early emotional differences.

The effect for fearful faces was mostly seen at lateral-posterior sites (and to a lesser extent at occipital sites) and emerged ~150ms during the descending part of the N170 toward the P2 component. It peaked around 180-200ms, and was significantly different from happy and neutral faces until 300ms (Fig.4-6, Table 5). The distribution of this fearful effect across the scalp was similar to that reported by Eimer and Holmes (2002; topographic maps of that study reported in Eimer and Holmes, 2007), with bilateral posterior-temporal negativities along with a fronto-central positivity. Eimer and Holmes (2002) however reported this effect starting around 110-120ms, i.e., earlier than in the present study, and suggested the involvement of frontal brain areas. In contrast, as most of the present effects were seen at posterior sites, we believe that the frontal distribution is mostly the positive counterpart of a posterior negativity that is likely coming from posterior visual brain regions. At these lateral-posterior sites, this negativity never interacted with fixation location and thus seems to reflect activity linked to the processing of fear added onto the normal activity related to processing neutral faces, as proposed by other groups (Schacht & Sommer, 2009; Rellecke et al., 2013). This added negativity started around the same time as the N170 but was seen mostly after the peak, and again did not interact with the fixation location, suggesting it was different from the structural encoding reflected by the N170 component.

This fearful effect was thus seen right after the N170 until around 300ms and encompassed the visual P2 (~200ms) component and the well-known marker of emotion

processing EPN (Rellecke et al., 2013; Rellecke et al., 2011; Schupp et al., 2004). These results are in line with previous reports of emotion effects starting around or right after the N170 and lasting 100ms or more (Eimer et al., 2003; Eimer & Kiss, 2007; Leppänen et al., 2007; Schupp et al., 2004; Sprengelmeyer & Jentzsch, 2006), here until about 300ms. This added negativity related to the processing of fear has been suggested to arise from an enhanced processing of emotionally salient stimuli in cortical visual areas involved in the perception of emotionally salient stimuli (Schupps et al., 2004). The timing of this fear-related process coincides with amygdala activation reported in intracranial ERP studies in response to fearful faces ~150-200ms post-stimulus (Meletti et al., 2012; Krolak & Salmon, 2004; Pourtois, Spinelli, Seeck, & Vuilleumier, 2010a) as well as in a recent MEG study (Dumas et al., 2013).

2.4.5 Conclusion

To summarize and conclude, in this gender discrimination task where facial expressions were task-irrelevant, differential effects of fixation location and emotion were seen across various ERP components. A sensitivity to face position was seen early, on the P1 component. An eye sensitivity that was independent of the emotion expressed by the face was seen on the N170 component, possibly reflecting the activity of an eye-detector in the processing of the face structure. The N170 peak was not sensitive to emotion; however, effects were seen for fearful faces right after the peak. A happy effect was seen at occipital sites that started around 100ms and lasted until 350ms. For fearful faces, an effect was seen around 50-100ms localized to the left hemisphere at lateral-posterior sites followed by a later effect bilaterally from 150 to 300ms, although stronger on the left hemisphere between 250 and 350ms. Results suggest happy and fearful expressions recruit different spatio-temporal networks with distinctive scalp distributions.

Results also highlight the importance of quantifying neural activity around P1 and N170 peaks as emotion effects may be missed by simply measuring these commonly studied ERP markers.

Chapter 3: Fixation to features and neural processing of fearful and happy facial expressions in an explicit emotion discrimination task (Experiment 2)[9]

3.1 Introduction

Research has pointed to the importance of different facial features for the recognition of different emotions. Calder, Young, Keane, and Dean (2000) showed that the top half of the face was most important for accurate recognition of fearful and angry expressions whereas the bottom half of the face was most important for happy expressions. Visual scanning studies have also shown expression specific saccadic eye movements, with equivalent saccades to the eyes and mouth for fear and mostly to the mouth for happiness (Eisenbarth, & Alpers, 2011). Studies using the *Bubbles* method (Smith, Gosselin, Cottrell, & Schyns, 2005; Schyns, Petro, & Smith 2007) identified specific facial features underlying the correct categorization of basic emotions. The smiling mouth is the critical diagnostic cue for happy expression categorization and wide open eyes for the categorization of fearful expressions. Studies combining the *Bubbles* method with EEG have suggested that the N170 peaks when the expression-specific diagnostic facial feature is encoded. Importantly, the "diagnostic feature" hypothesis implies that these expression-specific diagnostic facial features are required for tasks requiring emotion categorization. In fact, the diagnostic feature framework suggests that different features might be used depending on task demands (Schyns et al., 2003, 2007, 2009; Smith & Merlusca, 2014). Each categorization task (e.g., gender, identity, facial expression) is associated with its own diagnostic cues, which are

[9] A version of this chapter and chapter 4 combined, will be submitted to *Biological Psychology* (Neath & Itier, in prep)

attended to and processed in order for correct categorization of that stimulus (Schyns, Bonnar, & Gosselin, 2002).

In the current thesis, Exp. 1 tested the impact of facial features on the neural response to whole fearful and happy expressions during a gender discrimination task (GD) and specifically, whether fixation to the eyes of fearful faces was driving previous reports of an enhanced N170 to fearful faces. Using an eye-tracker and a gaze-contingent procedure to enforce fixation on facial features of fearful, happy and neutral expressions, Exp. 1 (GD) revealed different spatio-temporal emotion effects for happy and fearful faces that were largely independent of fixation location. A weak interaction of emotion with fixation location was seen at occipital sites only during 150-200ms, with smaller amplitudes for both happy and fearful faces compared to neutral faces seen only when fixation was on the mouth. Thus, although limited temporally, these interactions between emotion and fixation location suggested a possibly important role of the mouth in processing both happy and fearful faces, while fixation to the eyes did not yield the predicted specific effects for the processing of fearful faces. However, this lack of interaction between fearful expressions and fixation to the eyes may be the result of using a GD task, which was emotion-irrelevant, as previous studies reporting modulation of the neural response to facial expressions have employed emotion discrimination (ED) tasks (e.g., Leppänen et al., 2008; Schyns et al., 2007, 2009). If diagnostic facial features are tied to explicit emotion discrimination, I would expect to see an interaction between emotion and expression-specific diagnostic facial features during a task requiring emotion categorization. Therefore, following up on Expt.1 (GD), Exp.2 tested the impact of fixation to facial features on the neural processing of facial emotions during an ED task.

In the present study, fearful, happy and neutral faces were again presented with fixation to the left eye, right eye, nose and mouth using the same gaze-contingent design as Exp. 1. A replication of Exp.1 regarding stimulus position effects on the P1 was expected, as well as the larger N170 amplitude for fixation to the eyes compared to the nose and mouth. I also hoped to reproduce the distinct spatio-temporal pattern of fearful and happy effects found in Exp.1. I expected that the task demands in the explicit emotion discrimination task would impact the fixation and emotion interactions such that an enhanced fearful effect would be seen for fixation to the eyes compared to the nose or mouth and a larger happy effect would be seen for fixation to the mouth compared to the eyes or nose, given the respective "diagnosticity" of these features for the two emotions. The interactions were expected around the timing of the N170 or later (onset of the semantic processing of facial emotions as seen in Exp. 1 during the timing coinciding with the EPN).

3.2 Methods

3.2.1 Participants

Forty-seven undergraduate students from the University of Waterloo (UW) were recruited and received course credit for their participation. They all lived in North America for at least 10 years and reported normal or corrected-to-normal vision, no history of head-injury or neurological disease, and were not taking any medication. They all signed informed written consent and the study was approved by the Research Ethics Board at UW. At the start of the study, calibration of the eye-tracker failed for 8 participants who were not further tested. The remaining 39 participants were tested but 19 were rejected for the following reasons. One participant completed less than half of the study; four were removed due to artefacts resulting

in many conditions with fewer than our 40 trials per condition cut-off (50% of the initial trials per condition); 13 had too few trials after removing trials with eye movements outside of our defined fixation location region of interest of 1.4° of visual angle; one participant was rejected due to problems during EEG recordings. The results from 20 participants were kept in the final analysis (21 ± 3.1 years, all right-handed, 10 females).

3.2.2 Stimuli

Identical to Exp. 1 (refer to Table 2 on pg. 21 for PI and RMS contrast).

3.2.3 Apparatus and Procedure

Identical to Exp. 1 except for the task instructions. Participants were instructed to fixate on the black fixation-cross in the center of the screen in order to initiate each trial and to not move their eyes until the response screen appeared. To ensure that participants' fixation was on the cross, a fixation contingent trigger enforced the fixation on the cross for 307ms. Due to sensitivity of the eye-tracker, on average participants took 728ms (926.02 S.D) between the onset of the fixation-cross and the stimulus presentation. The target face stimulus was then presented for 257ms, immediately followed by the response screen displaying a vertical list of the three emotions (emotion word order counterbalanced between participants). The response screen remained until the response. Participants were instructed to categorize faces by their emotion as quickly and accurately as possible using a mouse by clicking on the appropriate emotion label. They were instructed to keep their hand on the mouse during the entire experiment to avoid unnecessary delays. On average, it took participants 1293ms (256.6ms S.D.) to respond. After their response, a screen appeared that read "BLINK" for 507ms. Participants were instructed to blink during this time to prevent eye movement artifacts during the first 500ms of trial recording.

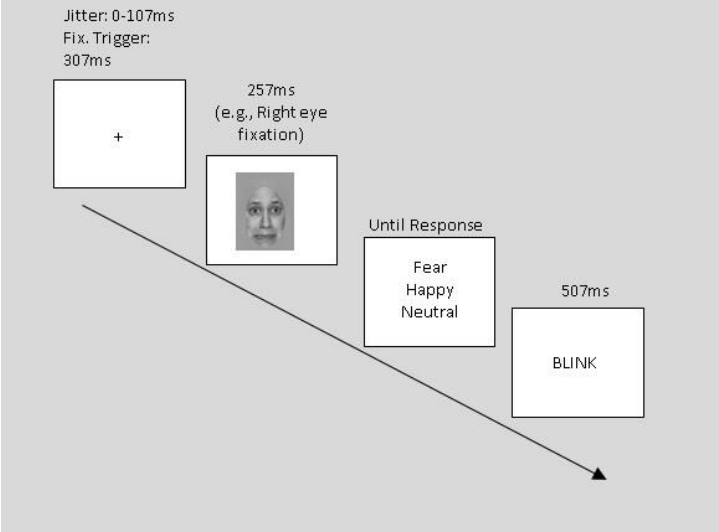


Figure 7. Emotion Discrimination Trial Sequence (Exp.2)

Trial example with right eye fixation and fearful expression. First a fixation point was displayed on the screen for a jittered amount of time (0-107ms) with an additional fixation trigger of 307ms. Following this, a grayscale picture was flashed for 257ms. A response screen immediately followed the stimulus and displayed a vertical list of emotions; participants selected, using a mouse, the correct emotion label that the face was expressing. The response screen remained until the participant's response, followed by a blink screen for 507ms.

3.2.4 Electrophysiological Recordings

Identical to Exp. 1 (cf. section 2.2.4 pg. 25).

3.2.5 Eye-Tracking Recordings

Identical to Exp. 1 (cf. section 2.2.5 pg. 25).

3.2.6 Data Processing and Analyses

Each trial was categorized as correct or incorrect based on the emotion categorization and only correct response trials were used for further analysis. In addition, for each participant we also kept trials in which RTs were within 2.5 S.D. from the mean of each condition (Van Selst & Jolicoeur, 1994) as a way to eliminate anticipatory responses (which could overlap with EPN component) or late responses, which excluded 7.05% of the total number of trials across the 20 participants. As done in Exp.1 and to ensure foveation to defined fixation location areas (left eye,

right eye, nose and mouth), trials in which a saccadic eye movement was recorded beyond 1.4° visual angle (70 pixels) around the fixation-location were removed from further analysis. An average of 3.29% of trials were removed during this step across the 20 participants included in the final sample.

The ERP data were processed offline in the same way as for Exp.1 (cf. section 2.2.6 pg. 25). Epochs were 500ms long (100ms pre-stimulus baseline) and digitally band-pass filtered off line (0.01–30Hz). Trials were rejected using an automated procedure when containing artifacts >±70μV, then visually inspected and further rejected if necessary. After eye movements and artefact rejection, participants with less than 40 trials in any condition (out of 80 initial trials) were rejected (the average number of trials per condition did not significantly differ across emotions (p = .35) or fixation location (p = .20)) (see Appendix A2 for the final number of trials per condition).

ERP Analyses. Using automatic peak detection, the P1 component was measured between 80 and 130ms post-stimulus-onset (peak around 100ms) at electrodes O1 and O2. Careful inspection of the data suggested emotion differences on P1 at Oz so P1 was also analyzed at Oz separately (as done in Exp. 1). The N170 peak was measured between 120-200ms at the electrode where it was maximal for each subject and for each hemisphere (see Table 6). Mean amplitudes were also calculated within 50ms windows starting from 50 to 350ms, separately for occipital sites (O1, O2 and Oz) and lateral-posterior sites (CB1/2, P9/10, P7/8 and PO7/8).

Table 6. *Number of subjects in Exp. 2 for whom the N170 was maximal at left (P9, CB1, PO7, O1) and right (P10, CB2, P08, O2) hemisphere electrodes. LH: left hemisphere; RH: right hemisphere.*

	LH		RH
P9	11	P10	14
CB1	6	CB2	4
PO7	2	PO8	1
O1	1	O2	1
Total n	20		20

Repeated-measure ANOVAs were conducted separately for correct categorization and ERP amplitudes using SPSS Statistics 22. Within-subject factors included hemisphere (2: left, right), emotion (3: fear, happiness, neutral) and fixation location (4: left eye, right eye, nose, mouth) for P1 and N170 peaks. For mean amplitudes, electrode was another factor (3 occipital sites: O1, O2, Oz; 4 lateral-posterior sites: CB1/2, P9/10, P7/8, PO7/8). If necessary further analyses of the interactions found were completed with separate ANOVAs for each fixation location or each emotion. All ANOVAs used Greenhouse-Geisser adjusted degrees of freedom and pairwise comparisons used Bonferroni corrections for multiple comparisons.

3.3 Results

3.3.1 Behavioural Analyses

The overall correct categorization rate was very good (≥ 80%, Table 7). Overall, participants made fewer correct responses for neutral than happy or fearful faces (main effect of emotion, $F(1.61, 30.67) = 3.98$, $p < .05$, $\eta_p^2 = .17$; significant neutral-happy paired comparison at $p < .05$). Correct responses were also slightly better for nose and mouth fixations compared to eye fixations (main effect of fixation location, $F(2.35, 44.67) = 18.01$, $p < .005$, $\eta_p^2 = .24$; left eye-

nose and left eye-mouth paired comparisons at $p < .05$). No emotion by fixation location interaction was seen.

Table 7. *Mean correct responses for fearful, happy and neutral expressions presented during the emotion discrimination task in Exp. 2 (standard errors to the means in parenthesis).*

		Mean (%) Correct in ED task (std. error)			
	Overall	Left Eye	Right Eye	Nose	Mouth
Fearful	**90.0** **(1.0)**	87.4 (1.2)	90.8 (1.2)	90.0 (1.0)	97.0 (1.2)
Happy	**91.4** **(1.0)**	90.7 (0.8)	91.4 (1.1)	91.6 (0.9)	91.7 (1.1)
Neutral	**88.4** **(1.0)**	85.9 (1.9)	87.5 (1.8)	88.8 (1.2)	91.4 (1.0)
Overall		**88.0** **(1.0)**	**89.9** **(1.0)**	**90.5** **(1.0)**	**91.3** **(1.0)**

3.3.2 ERP Analyses

3.3.2.1 Effects of fixation location and emotion at occipital sites (O1, O2, Oz)

P1 Peak Amplitude. For O1/2 sites, overall largest P1 amplitude was found for fixation to the mouth (main effect of fixation, $F(2.22, 42.21) = 26.32$, $p < .0001$, $\eta_p^2 = .58$) (see Fig. 8A). Fixation location also interacted with hemisphere ($F(2.07, 39.27) = 10.24$, $p < .0001$, $\eta_p^2 = .35$) due to opposite hemispheric effects for fixation to each eye. On the left hemisphere (O1), P1 was larger for the mouth and left eye (which did not differ significantly) compared to the right eye and the nose fixations (which did not differ) ($F = 27.75$, $p < .0001$, significant paired comparisons at $p < .0001$). On the right hemisphere (O2), P1 was larger for the mouth and right eye (which did not differ significantly) compared to the left eye and nose fixations which did not differ ($F = 14.45$, $p < .0001$; significant paired comparisons $p < .001$). A small three-way interaction between hemisphere, fixation location and emotion was found ($F(3.11, 59.1) = 3.25$, $p=.027$, $\eta_p^2 = .14$),

however, no effect of emotion or interaction with emotion was found when each hemisphere was analyzed separately and no clear pattern was seen.

At Oz electrode, P1 was also larger for fixation to the mouth compared to the left eye, right eye and nose which did not differ significantly from each other (main effect of fixation location, $F(2.04, 38.71) = 34.62$, $p < .0001$, $\eta_p^2 = .65$; significant paired comparisons with mouth fixation at $p < .001$) (Fig. 8A). Importantly, an effect of emotion was found due to a reduced positivity for happy compared to neutral expressions (main effect of emotion, $F(1.98, 37.65) = 5.74$, $p < .01$, $\eta_p^2 = .23$; happy-neutral paired comparison $p = .013$) (see Fig 8B). This happy effect was best seen by difference waveforms (happy-neutral) and was largest right after the P1, around 115ms (Fig. 8B and map). This effect was confirmed statistically with mean amplitude analyzes during the 100-150ms window (discussed below).

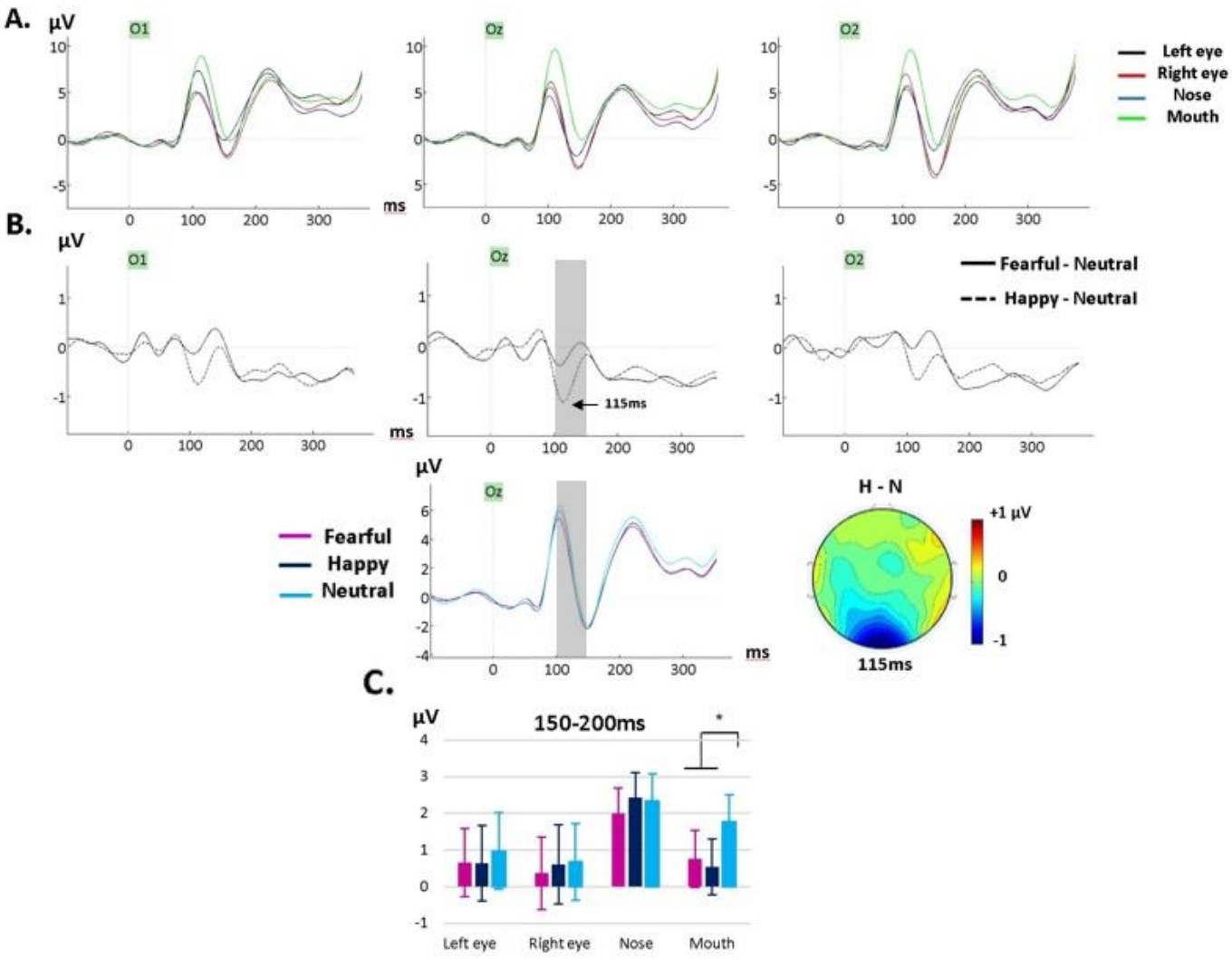
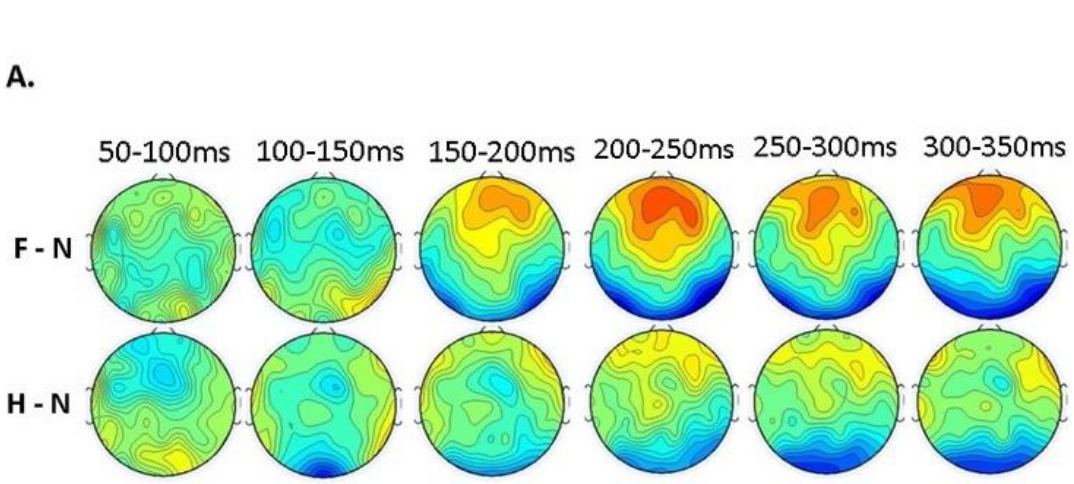


Figure 8. Effects of Fixation Location and Emotion at Occipital Sites (Exp.2)

(A) Grand-averages featuring the P1 component for Exp. 2 (ED) for neutral faces at O1, O2, and Oz electrodes, showing effects of fixations with larger amplitudes for mouth fixation and opposite hemispheric effects for eye fixations. (B) Grand-average difference waveforms generated by subtracting ERPs to neutral faces from ERPs to fearful faces (F-N, solid line) and ERPs to neutral faces from ERPs to happy faces (H-N, dashed line) at Oz (across fixation locations). A clear difference peak for happy-neutral was seen between 100-150ms at Oz and O2 (light gray band, peak of the "happy effect" around 115ms, see topographic map) and was confirmed by mean amplitude analysis at occipital sites during that time window (see main text and Table 8). The grand-averaged waveforms for fearful, happy and neutral faces (across fixation locations) at Oz clearly show that this "happy effect" started on the P1 peak. (C) Between 150-200ms, both happy and fearful effects were seen at occipital sites for the mouth fixation condition only (smaller amplitudes for emotional than neutral faces) as shown by the bar graph.

Table 8. *Exp. 2 (ED task) statistical effects on mean amplitudes analyzed over six 50ms time windows at occipital sites (O1, Oz, O2), with F, p and η_p^2 values. LH, left hemisphere; RH, right hemisphere; LE, left eye; RE, right eye; No, nose; Mo, mouth; F, fear; H, happy; N, neutral. Main effects p values: p* < .05; p** < .01; p*** < .001; p**** < .0001; ns, not significant. Significant Bonferroni-corrected paired comparison tests (p < .05) are also reported (e.g., H < F + N means that mean amplitude for happy was significantly smaller compared to both fearful and neutral expressions, while H + F < N means that mean amplitudes for both happy and fearful faces were significantly smaller than to neutral expressions). Effects reported in italics in parenthesis are effects that were weak and not clear and thus were treated as non-significant and not discussed in the text.*

Main effects and interactions	50-100ms	100- 150ms	150- 200ms	200-250ms	250-300ms	300-350ms
Electrode	-	-	-	*F* = 3.71, *p** , η_p^2 = .16 O1 > Oz	*F* = 4.45, *p**, η_p^2 = .19 O1 + O2 > Oz	*F* = 3.99, *p**, η_p^2 = .17 O1 > Oz
Fixation location	-	*F* = 35.25, *p****, η_p^2 = .65 Mo > all and LE > RE	*F* = 4.19, *p**, η_p^2 = .18 Pairwise comparisons ns	-	-	-
Emotion	-	*F* =7.09, *p***, η_p^2 = .27 H < F + N	*F* = 9.32, *p***, η_p^2 = .33 H + F < N	*F* = 11.6, *p****, η_p^2 = .38 H + F < N	*F* = 12, *p***, η_p^2 = .39 H + F < N	*F* = 15.35, *p****, η_p^2 = .45 H + F < N
Electrode X Fixation location	*(F = 4.92, p**, η_p^2 = .21* • *O1: ns* • *O2: ns* • *Oz: ns)*	*F* = 4.72, *p***, η_p^2 = .19 • O1: *F* = 31.13, *p****, η_p^2 = .62 Mo > LE > No + RE • O2: *F* =20.08 *p****, η_p^2 = .51 Mo > all • Oz: *F* 37.35, *p****, η_p^2 = .66 Mo > all and LE > RE	*F* = 3.82, *p**, η_p^2 = .17 • O1: *F* =4.17, *p**, η_p^2 = .18 No > RE • O2: *F* 5.51 *p***, η_p^2 = .23 No > LE + Mo • Oz: ns	*(F = 4.3, p**, η_p^2 = .18* • *O1: ns* • *O2: ns* • *Oz: ns)*	*(F = 3.55, p*, η_p^2 = .16* • *O1: ns* • *O2: ns* • *Oz: ns)*	-
Emotion X Fixation location	-	-	*F*= 3.50, *p***, η_p^2 = .16 • Mo: *F* =14.52, *p****, η_p^2 = .43 H + F < N • No: ns • LE: ns • RE: ns	-	-	-



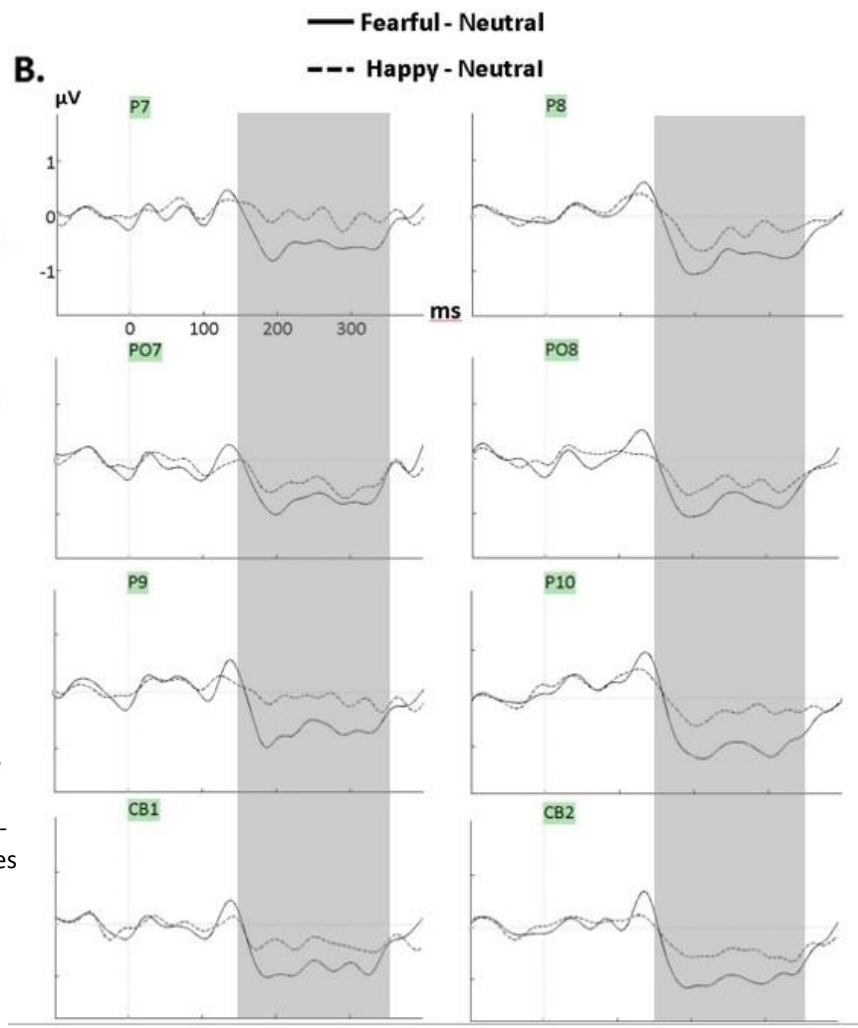


Figure 9. 2D Topographical Maps of Fearful-Neutral and Happy-Neutral Voltage Differences (Exp. 2)

A) Mean voltage distribution maps of the grand-average difference waveforms between fear and neutral (F-N) and happy and neutral faces (H-N) across six 50ms time intervals from 50ms to 350ms (averaged across fixation location) in Experiment 2 (ED task). The early occipital effect for happy is clearly seen between 100-150ms while the fearful effect starts at 150-200ms. Different topographies are seen for the two emotions with an occipital distribution for the happy effect and a more lateral-posterior distribution for the fearful effect (with positivity at frontal sites). (B) Grand-average difference waveforms (F-N and H-N, across fixation locations) at lateral-posterior sites (P7/8, PO7/8, P9/10, CB1/2). The gray zones indicates the time during which significant emotion effects were seen at all lateral-posterior sites (150-350ms, see Table 9).

Mean Amplitudes over Six Time Windows (O1, O2, Oz). Statistical results for these analyses (50-350ms) are reported in Table 8 and visually depicted in Figures 8 and 9.

More positive amplitudes were seen when fixation was to the mouth compared to the other facial features between 100 and 150ms, and this effect was strongest at Oz (electrode x fixation location interaction, Table 8). For O1 and Oz, larger amplitudes for left eye fixation than right eye fixation was also seen, reminiscent of the hemisphere by fixation effect seen on the P1 peak. Between 150 and 200ms, overall more positive amplitudes during fixation to the nose were seen at O1 and Oz (electrode by fixation location). After 200ms, no more fixation location effect was seen.

An emotion effect was first seen during the 100-150ms time window with smaller amplitudes for happy compared to neutral (and fearful) expressions (Fig. 8B) confirming the happy effect found on P1 at Oz reported previously. At 150-200ms smaller amplitudes were now seen for both fearful and happy compared to neutral expressions; however, a significant emotion by fixation location interaction revealed this was only seen for the mouth fixation condition (Figure 8C bar graph). From 200 to 350ms both fearful and happy expressions elicited smaller amplitudes compared to neutral expressions regardless of fixation location.

To summarize, a happy effect was seen at occipital sites from ~100 until 350ms, as clearly seen on the difference waveforms and their topographic maps (Fig. 9A, see also Fig. 8B). A Fearful effect was seen a bit later, starting at 150ms until 350ms. Interestingly, from 150 to 200ms both emotion effects occurred only during fixation to the mouth. Figure 9A also suggests that the fear effect was mostly lateral (as discussed next) and less occipital, while the opposite was found for happy faces.

3.3.2.2 Effects of fixation location and emotion at lateral-posterior sites (CB1/2, P9/10, P7/8, PO7/8)

N170 Peak Amplitude. The N170 amplitude was larger for fixation to the left and right eyes (which did not differ) compared to fixation to the mouth and nose which did not differ significantly (main effect of fixation location, $F(1.49, 28.29) = 12.63$, $p < .0001$, $\eta_p^2 = .40$; all paired comparisons at p-values < .01) (Fig. 10A). This fixation effect was more pronounced on the right than on the left hemisphere (hemisphere by fixation location, $F(1.57, 29.84) = 3.61$, $p<.05$, $\eta_p^2 = .56$). The N170 amplitude was also larger in the right compared to the left hemisphere (main effect of hemisphere, $F(1, 19) = 8.52$, $p < .01$, $\eta_p^2 = .31$). No effects of emotion or emotion by fixation location interaction were seen.

P1-to-N170 amplitude. As done in Exp.1, peak-to-peak analyses were performed to track possible influences of P1 onto N170 measures at these lateral sites. Thus, P1 was measured again at the electrodes at which the N170 was largest for each hemisphere and each subject and the amplitude differences between the P1 and the N170 at these sites was then calculated. Amplitude differences were larger in the right compared to the left hemisphere (main effect of hemisphere, $F(1, 19) = 19.94$, $p < .0001$, $\eta_p^2 = 51$). There was also a main effect of fixation location, ($F(1.95, 37.11) = 33.28$, $p < .0001$, $\eta_p^2 = .64$), due to larger amplitudes for the eyes than for the nose and mouth, reproducing the effect of fixation location seen on the N170.

Table 9. *Exp. 2 (Emotion discrimination task) statistical effects on mean amplitudes analyzed over six 50ms time windows at lateral-posterior sites (CB1/2, P7/8, PO7/8, P9/10), with F, p and ηp^2 values. LH, left hemisphere; RH, right hemisphere; LE, left eye; RE, right eye; No, nose; Mo, mouth; F, fear; H, happy; N, neutral. Main effects p values: p* < .05; p** < .01; p*** < .001; p**** < .0001; ns, not significant. Bonferroni-corrected significant paired comparison tests (p<.05) are also reported (e.g., F < H + N means that mean amplitude for fearful faces was significantly smaller compared to both happy and neutral expressions, while F + H < N means that mean amplitudes for both fearful and happy faces were significantly smaller than to neutral expressions).*

Main effects and interactions	50-100ms	100- 150ms	150- 200ms	200-250ms	250-300ms	300-350ms
Electrode	-	*F* = 25.65, *p*****, η_p^2 = .57 P9/10 < CB1/2 + P7/8 < PO7/8	*F* =42.96, *p*****, η_p^2 = .69 P9/10 < CB1/2 + P7/8 < PO7/8	*F* = 36.37, *p*****, η_p^2 = .66 P9/10 < CB1/2 < P7/8 < PO7/8	*F* = 42.21, *p*****, η_p^2 = .69 P9/10 + CB1/2 < P7/8 < PO7/8	*F* = 39.54, *p*****, η_p^2 = .68 P9/10 < CB1/2 + P7/8 < PO7/8
Fixation location	-	*F* = 9.63, *p****, η_p^2 = .34 RE + No < LE + Mo	*F* = 21.17, *p*****, η_p^2 = .53 All < No	*F* = 8.25, *p****, η_p^2 = .30 All < No	-	-
Emotion	-	-	*F* = 26.60, *p*****, η_p^2 = .58 F < H < N	*F* = 42.89, *p*****, η_p^2 = .66 F < H < N	*F* = 16.94, *p*****, η_p^2 = .47 F < H + N	*F* = 19.05, *p*****, η_p^2 = .50 F < H < N
Emotion X Electrode	*(F = 3.05, p*, η_p^2 = .14* • *CB: ns* • *P9/10: ns* • *P7/8: ns* • *P07/08: ns)*	-	-	-	-	-
Hemisphere X Fixation location	*F = 7.00, p**, η_p^2 = .27* • *LH: F = 4.20, p*, η_p^2 = .18* *Pairwise comparisons ns* • *RH: F = 3.48, p*, η_p^2 = .16* *Pairwise comparisons ns*	*F* =12.54, *p****, η_p^2 = .29 • LH: *F* = 12.54, *p****, η_p^2 = .39 No + RE < LE • RH: *F* = 5.19, *p***, η_p^2 = .22 No < Mo	*F* = 6.19, *p***, η_p^2 = .53 • LH: *F* = 11.31, *p***, η_p^2 = .37 LE + RE < No • RH: *F* = 18.39, *p***, η_p^2 = .45 LE + RE (<) Mo < No	*F* = 3.61, *p**, η_p^2 = .16 • LH: *F* = 3.80, *p**, η_p^2 = .17 RE < No • RH: *F* = 6.66, *p***, η_p^2 = .26 All < No	*(F = 3.56, p**, η_p^2 = .16* • *LH: ns* • *RH: ns)*	-
Hemisphere X Emotion	-	-	-	*F* = 3.48, *p**, η_p^2 = .05 • LH: *F* =29.39, *p****, η_p^2 = .61; F < H + N • RH: *F* =29.34, *p****, η_p^2 = .61; F < H < N	-	-
Emotion X Fixation location	-	-	-	-	*F* = 3.21, *p**, η_p^2 = .15 • LE: *F* = 15.12, *p****, η_p^2 = .44; F < H + N • RE: *F* = 14.60, *p****, η_p^2 = .44; F < H + N • No: no effect • Mo: *F* = 6.43, *p***, η_p^2 = .25; F + H < N	*F* =2.77, *p**, η_p^2 = .13 • LE: *F* =8.60, *p***, η_p^2 = .31; F < H + N • RE: *F* = 12.36, *p****, η_p^2 = .39; F < H + N • No: no effect Mo: *F* = 9.68, *p***, η_p^2 = .34; F+H < N
Hemisphere X Emotion X Fixation location	-	*F* = 3.19, *p**, η_p^2 = .14 • LH: no emotion effect • RH: emo x fix, *F* = 3.35, *p**, η_p^2 = .15 LE: *F* = 8.71, *p***, η_p^2 = .31; H > N No: *F* =5.07, *p**, η_p^2 = .21 F > H RE: ns Mo: ns	-	-	-	

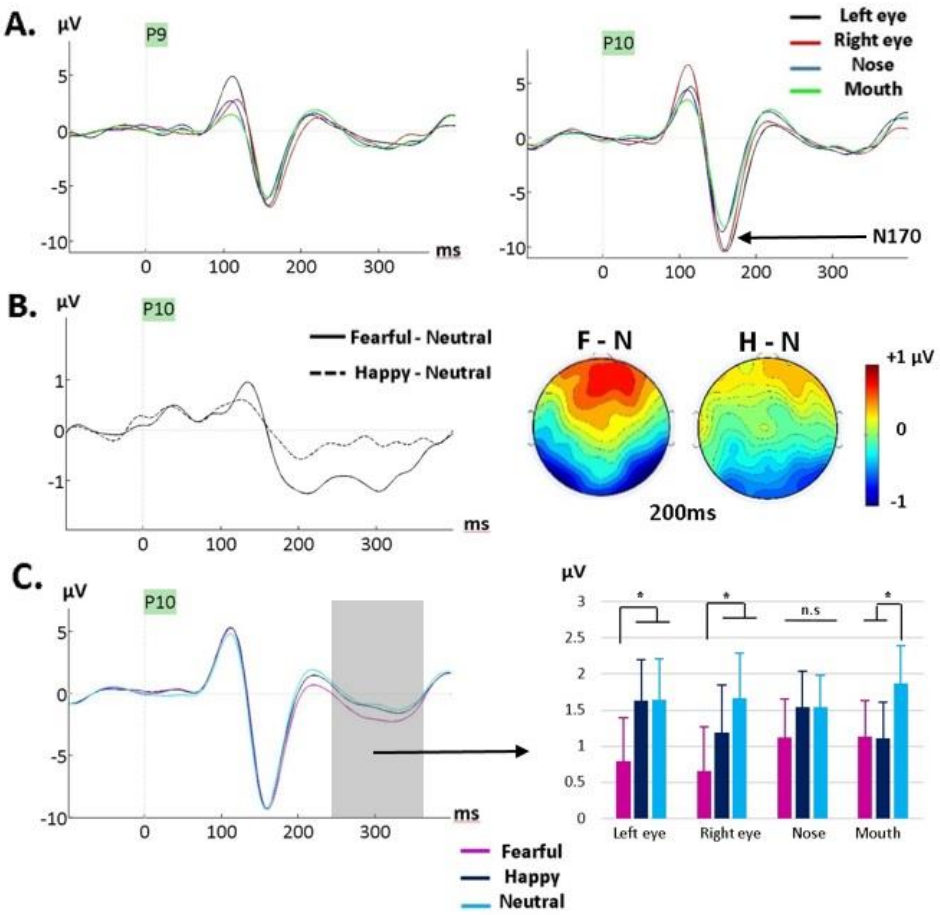


Figure 10. Effects of Fixation Location and Emotion at Lateral-Posterior Sites (Exp.2)

(A) Grand-averages featuring the N170 component for neutral faces at P9 and P10 as a function of fixation location during Exp. 2 (ED task). (B) Grand-average difference waveforms generated by subtracting ERPs to neutral from ERPs to fearful faces (F-N, solid line) and ERPs to neutral from ERPs to happy faces (H-N, dashed line) at P10. The maps show the voltage difference between fearful and neutral faces (F-N) and happy and neutral (H-N) at 200ms post-stimulus, when the fearful effect was largest. (C) Grand-averages for fearful, happy and neutral faces (across fixation locations) at P10 site where the effect was clearly seen. The gray interval over 250-350ms is where an emotion by fixation interaction was seen; the bar graph depicts the mean amplitudes averaged across 250-300 and 300-350ms intervals. Smaller amplitudes for fearful compared to both happy and neutral faces were seen for both eyes fixations while for the mouth fixation, smaller amplitudes were seen for both fearful and happy faces compared to neutral faces.

Fixation location also interacted with hemisphere ($F(2.78, 52.95) = 7.42$, $p < .0001$, $\eta_p^2 = .46$) due to different effects of the eyes on each hemisphere: on the left hemisphere, amplitude for the left eye was larger than for the right eye ($p = .002$) while on the right hemisphere, amplitude for both eye fixations did not differ.

Interestingly, there was also a significant main effect of emotion ($F(1.99, 37.86) = 3.63$, $p=.036$, $\eta_p^2 = .16$) that interacted with fixation location ($F(3.84, 72.97) = 2.87$, $p = .031$, $\eta_p^2 = .13$) due to a larger P1-N170 amplitude difference for happy faces compared to neutral (and fearful) faces that was seen only when fixation was on the mouth (mouth: effect of emotion, $F = 6.24$, $p < .01$, $\eta_p^2 = .25$; significant happy-neutral paired comparisons $p < .05$). There was no effect of emotion when fixation was on the left eye ($p = .32$), right eye ($p = .94$) or nose ($p = .36$). This interaction was also seen in Exp.1 for P1-N170 analysis although only on the left hemisphere, and is similar to the emotion by fixation location interaction seen for happy faces between 150 and 200ms at occipital sites (Fig.10C, Table 8). Thus, when fixation was on the mouth, the happy effect started between the P1 and N170 peaks at lateral sites.

Mean Amplitude analyses over Six Time Windows (CB1/2, P7/8, P9/10, PO7/8).

Statistical results for these analyses (50-350ms) are reported in Table 9 and visually depicted in Figures 9 and 10.

Between 100 and 150ms (which encompassed the P1), fixation location interacted with hemisphere (Table 9) such that on the left hemisphere, mean amplitudes were smaller for the nose and right eye fixation compared to the left eye fixation, while on the right hemisphere, amplitudes were significantly smaller for the nose than the mouth fixation. Between 150 and 250ms, the mean amplitudes were most negative for the eyes and least negative for nose (main effect of fixation and hemisphere by fixation location interactions, Table 9). No effect of fixation location was seen after 250ms (the hemisphere by fixation location interaction seen during the 250-300ms time window did not reveal any clear pattern).

An effect of emotion was first seen at 100-150ms in a small three-way interaction between hemisphere, emotion and fixation location. No emotion effect was seen in the left hemisphere. For the right hemisphere, emotion interacted with fixation location; however, no clear effects were seen. A main effect of emotion was seen between 150 and 350ms, with smaller amplitudes for fearful than neutral faces, best captured by difference waves and their topographies as a bilateral posterior negativity with positive counterpart at frontal sites (Fig.9); this fearful effect peaked around 200ms (Fig. 10B). During the same period, amplitudes were also smaller for happy than neutral faces although this happy effect was much weaker than the fear effect (Fig.9). Scalp topographies overall pointed at different underlying generators for the two emotion effects. Between 250 and 350ms, emotion interacted with fixation location (Table 9, Fig. 10C). The effect for fearful expressions was seen when fixation was on the eyes and mouth, but not when fixation was on the nose. The happy effect was only seen when fixation was on the mouth.

3.4 Discussion

Using the same gaze-contingent procedure as Exp.1, I investigated the effects of fixation to different facial features on the neural processing of fearful, happy and neutral facial expressions in an explicit discrimination (ED) task. Overall emotion categorization performance was very good, with a small recognition advantage for emotional relative to neutral expressions, and followed a similar pattern of behavioural performance as previously reported, where emotion recognition is typically better for happy compared to fearful expressions (e.g., Palermo & Coltheart, 2004; Tottenham et al., 2009). A categorization performance advantage was also seen during fixation to the nose and mouth compared to the eyes, supporting the idea of an

emotion recognition advantage from facial information in the bottom half of the face (e.g., Blais, Roy, Fiset, Arguin, & Gosselin, 2012).

As predicted, a clear fixation effect was seen on P1 peak (Figure 8A, Table 8) with larger amplitude when fixation was on the mouth compared to the eyes and nose. This effect was also seen between 100 and 150ms at occipital sites and likely reflected sensitivity to the face position on the screen, given that most facial information was in the upper visual field during fixation to the mouth, as discussed in Exp.1 (Section 2.4.2). P1 amplitude was also larger for the right eye than the left eye on the right hemisphere and larger for the left eye compared to the right eye on the left hemisphere. The larger amplitude for the left than the right eye was also captured by mean amplitude analyses between 100 and 150ms (at O1 for occipital sites and on the left hemisphere for posterior lateral sites), and by the P1-N170 amplitude difference analysis on the left hemisphere. This fixation effect reflects hemifield presentation effects as most of the facial information was in the left visual field when fixation was on the right eye and in the right visual field when fixation was on the left eye (see Fig.1). These effects are similar to the fixation effects reported in Exp. 1 (although were most pronounced in the left hemisphere) and by recent studies using similar gaze-contingent procedures (de Lissa et al., 2014; Nemrodov et al., 2014; Zerouali et al., 2013).

As also expected, replicating Exp.1, larger N170 amplitudes were found for both eye fixations compared to the nose and mouth fixations (de Lissa et al., 2014; Nemrodov et al., 2014). This larger amplitude for the eyes was also found with the mean amplitude analysis at posterior lateral sites between 150 and 200ms and supports the idea of a special role for the processing of eyes at the level of facial structural encoding. This N170 eye sensitivity was seen to the same

extent for the three facial expressions, as in Exp.1, and there was no effect of emotion on this component, consistent with previous ERP studies requiring discrimination of facial expressions (e.g., Leppänen et al., 2008; Schupp et al., 2004; however see Hinojosa, Mercado, & Carretié, 2015).

Like Exp. 1, smaller amplitudes for happy relative to neutral expressions started on the P1 and were seen mainly over occipital sites, ~100-350ms post-stimulus, while smaller amplitudes for fearful relative to neutral expressions started right after the N170, ~150-350ms post-stimulus mainly over posterior-lateral sites. The overall scalp distribution and timing of these happy and fearful effects were remarkably similar to Exp. 1 and support the idea of different neural generators underlying the processing of these two facial emotions.

The localized emotion by fixation location interaction at occipital sites seen in Exp.1 was also reproduced in the current study between 150 and 200ms post-stimulus onset (Table 8), with smaller amplitudes (less positive, more negative going) for both happy and fearful relative to neutral expressions seen only during fixation to the mouth. The impact of the mouth for happy expressions started in fact earlier, as revealed by the P1-N170 amplitude difference.

Novel to the current ED task was an emotion by fixation location interaction at lateral-posterior sites between 250 and 350ms (coinciding with EPN) with more negative amplitudes for fearful compared to neutral expressions when fixation was on either the eyes or the mouth but not on the nose (Table 9). During that time window, amplitudes were also smaller (more negative) for happy than neutral expressions only during fixation on the mouth, with no effects of emotion seen during fixation on the nose. Previous studies reporting emotional modulation of the EPN have used a central fixation (i.e., fixation landing on the nose or nasion). Given fixation

was not enforced in previous studies it is possible that participants made small shifts in gaze towards the eyes and nose driving the effects.

Previous studies of ERP modulations by expression-specific facial features have reported only the occipito-temporal distribution with larger N170 amplitudes for fearful eyes and happy mouths (e.g., Schyns et al., 2007, 2009; Calvo & Beltrán, 2014) and more negative-going response for fearful eyes beginning at the latency of the N170 until 240ms (encompassing the EPN; Leppänen et al., 2008). Systematic analyses including occipital and lateral-posterior sites in the current study revealed that the eyes impacted processing of fearful faces; however, the mouth impacted processing of both happy and fearful expressions. Information from the mouth may be required for early processing of happy faces (~115-120ms), seen mostly with an occipital distribution and to a lesser extent at lateral-posterior sites whereas processing of fearful expressions is seen later (~180ms) requiring information from the mouth and the eyes with a lateral-posterior distribution and to a lesser extent at occipital sites.

Albeit different, the present results indeed found support for the importance of diagnostic features at the neural level. In line with visual scanning studies (Eisenbarth & Alpers, 2011) the current study suggests that both the mouth and eyes are important for fearful faces, not just the eyes as suggested by others (e.g., Smith et al., 2005; Schyns et al., 2007, 2009). It is important to note, however, that these results might be specific to the current emotion discrimination task. Whether these features play an important role in the processing of fearful and happy expressions during tasks where less attention to the face is required (e.g., oddball detection) remains to be tested.

Chapter 4: Fixation to features and neural processing of fearful and happy facial expressions in an oddball task (Experiment 3)[10]

4.1 Introduction

In the current thesis, tasks requiring gender discrimination (GD, Exp.1) and explicit emotion discrimination (ED, Exp.2) revealed similar patterns of emotion effects with different scalp distributions for happy and fearful expressions. These emotion effects did not interact with fixation location at the N170 level, suggesting that the structural encoding of the face, and processing of emotion may take place at separate stages. In contrast, these emotion effects were found to interact with fixation to facial features before or after the N170 and the pattern of these interactions varied between the two experiments. However, a large proportion of published reports of enhanced P1 and N170 components for fearful (compared to neutral) expressions have occurred in tasks where emotional faces were viewed passively (e.g., Blau et al., 2007; Pizzagalli et al., 2002; Schupps et al., 2004) or in oddball detection tasks requiring a face vs. non-face judgment (e.g., Batty & Taylor, 2003; Leppänen et al., 2007; Williams et al., 2004). Therefore the current study tested the impact of fixation to facial features on the neural processing of fearful and happy expressions during an oddball detection task.

When participants were instructed to categorize face gender in Exp.1, emotion effects for fearful expressions occurred largely independently of fixation location. For happy expressions, however, there was a small interaction such that the happy effect at occipital sites was seen during fixation to the mouth only between 150 and 200ms, and that interaction was also

[10] A version of this chapter and chapter 3 combined, will be submitted to *Biological Psychology* (Neath & Itier, in prep)

significant with the P1-N170 peak difference analysis (on the left hemisphere) at posterior lateral electrodes. Importantly, this interaction was replicated in Exp. 2 when participants were explicitly instructed to discriminate between facial expressions. In Exp. 2 the interaction could once again be seen in the P1-N170 peak difference analysis and at occipital sites during the same time window. A novel interaction seen during Exp.2 (ED) occurred at lateral-posterior sites between 250 and 350ms (timing that coincides with the EPN) such that the fearful effect was seen during fixation to the eyes and the mouth but not during fixation to the nose, whereas a happy effect was seen only during fixation to the mouth (see bar graph on Fig.10). This suggests that fixation on these diagnostic cues impacted facial expression processing *after* the structural encoding of the face (as indexed by N170), during a time window coinciding with the processing of the emotional content (EPN, 250-350ms) during explicit emotion categorization. Facial features therefore impact the neural processing of fearful and happy expressions differently depending on task demands (i.e., gender vs. explicit emotion discrimination). Facial features may also impact facial expression processing differently during tasks requiring less attention to the face, an idea that I tested in Exp. 3 using an oddball (flower) detection task (ODD).

Using the same gaze-contingent procedure as Exp. 1 and 2, fixation to facial features was manipulated while participants were instructed to view a series of images and respond when they detected a flower thus making a face vs. flower judgment. Early P1 effects for fearful faces have been reported during oddball detection tasks (e.g., Batty & Taylor, 2003; Williams et al., 2004). When controlling for low-level stimulus characteristics (pixel intensity and RMS contrast), Exp.'s 1 (GD) and 2 (ED) found no effect of fear for the P1 and N170; however, it is possible that this early effect for fear may be revealed in the current oddball detection task since the task

requires that less attention be placed on the face. This would suggest earlier processing of fearful faces only during tasks requiring a face vs. non-face judgment, compared to tasks requiring accurate categorization of face gender and facial expression, further suggesting the effect is driven by attention to the face placed by task demands and not by emotion *per se*. Replication of the distinct emotion effects for happy (occipital distribution) and fearful (lateral-posterior) expressions seen in Exp.1 and 2 would suggest a general emotion effect regardless of task demands. It was also possible that these emotion effects would interact with fixation to facial features. Replication of the interaction of the early effect for happy with fixation to the mouth, seen in Exp.1 and 2, would suggest the effect was driven by the salient smiling mouth regardless of task. Emotion by fixation location interactions seen later (~200-350ms) as seen in Exp.2, would suggest these diagnostic features (i.e., mouth and eyes) are not solely tied to explicit emotion discrimination. It is to be noted, however, that the role of diagnostic facial features during facial expression processing has only been tested in tasks requiring emotion or gender categorization and therefore it was difficult to make concrete a priori predictions concerning whether emotion effects would interact with fixation to facial features in this oddball task.

4.2 Methods

4.2.1 Participants

Forty three-undergraduate students were tested at UW and received course credit. All participants lived in North America for at least 10 years and reported normal or corrected-to-normal vision, no history of head-injury or neurological disease, and were not taking any medication. They all signed informed written consent and the study was approved by the Research Ethics Board at UW Seventeen participants were rejected: two for completing less than

half of the experiment thus rendering too few trials per condition; five for too many trials with artefacts resulting in too few trials per condition; 10 due to too few trials remaining after removing trials with eye movements greater than 1.4° of visual angle from the fixation location (see Fig. 1); and two due to high anxiety (scores higher than 43 on the STICSA, Ree et al. 2008). The results from 26 participants were kept in the final analysis (20.8 ± 1.7 years, 15 female, 22 right-handed).

4.2.2 Stimuli

The face stimuli were the same as those used in Exp.'s 1 and 2. In addition, 6 flower images were used as oddball stimuli. To be consistent with the face images, all flower stimuli were converted to grayscale in Adobe™ Photoshop CS5 and an elliptical mask was applied (see Fig.11). As in Exp. 1 and 2, a unique central fixation-cross was used and each face was presented offset so the pre-determined center of each feature would land on the center of the fixation-cross. To keep in line with the experimental paradigm, coordinates corresponding to the left eye, right eye, nose and mouth of a randomly selected neutral face identity were used for all flower stimuli (see Fig. 1).

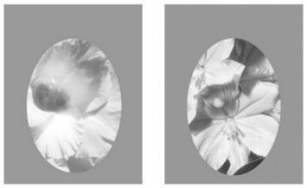


Figure 11. Oddball Flower Stimuli (Exp.3)

Example of oddball target flower stimuli used in Exp. 3.

4.2.3. Apparatus and Procedure

Participants completed an oddball detection task where they were instructed to press the space bar as quickly and accurately as possible to the target stimuli (flowers) which occurred

infrequently (20% of the time) amongst non-target stimuli (fearful, happy and neutral faces). Participants were given 8 practice trials. The experimental session used the same gaze-contingent procedure as in Exp. 1 except for the response screen (Fig. 12). On average participants took 880ms (781 S.D) between the onset of the fixation cross and the stimulus presentation. The stimulus was immediately followed by a fixation cross that was presented for 747ms after a face stimulus or until response after a flower stimulus. Participants were instructed to blink during this time. The experimental block contained 96 face trials (3 emotions X 4 fixation locations X 8 identities) and 24 flower trials (4 fixation locations X 6 flowers), and was repeated 10 times in a randomized order, yielding 80 trials per face condition, across the 10 blocks. Participants then completed the 21 item trait anxiety test from the STICSA.

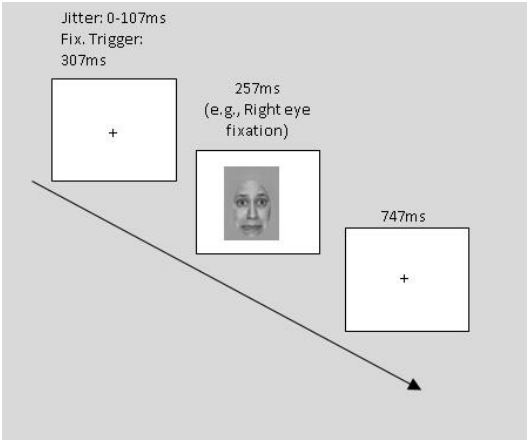


Figure 12. Oddball Detection Trial Sequence (Exp.3)

Trial example used in the Oddball task with right eye fixation and fearful expression. First a fixation point was displayed on the screen for a jittered amount of time (0-107ms) with an additional fixation trigger of 307ms. Following this, a grayscale picture was flashed for 257ms. The stimulus was followed by a fixation cross that was presented for 747ms for face trials or until response for flower trials.

4.2.3 Electrophysiological recordings

Identical to Exp.'s 1 and 2 (cf. section 2.2.4 pg. 25).

4.2.4 Eye-tracking recordings

Identical to Exp.'s 1 and 2 (cf. section 2.2.5 pg.25).

4.2.5 Data processing and analyses

Identical to Exp.'s 1 and 2 (cf. section 2.2.6 pg.25). In this task 6.8% of trials across the final 26 participants were removed due to eye movements recorded beyond 1.4° visual angle (70px) around the fixation location. The final trial number did not differ significantly by emotion (p = .17) or fixation location (p = .33) (see Appendix A3 for final number of trials per condition). As done in Exp.'s 1 and 2, the N170 peak was measured between 120-200ms at the electrode where it was maximal for each subject and for each hemisphere (see Table 10).

Table 10. *Number of subjects in Exp. 3 for whom the N170 was maximal at left (P9, CB1, PO7, O1, TP9) and right (P10, CB2, P08, P8, O2) hemisphere electrodes. LH: left hemisphere; RH: right hemisphere.*

	LH		RH
P9	10	P10	12
CB1	11	CB2	6
PO7	3	PO8	4
P7	-	P8	3
O1	1	O2	1
TP9	1	TP10	-
Total n	26		26

4.3 Results

4.3.1 Behavioural Analyses

Overall detection of flower stimuli was excellent (~98%) demonstrating that the participants were attending to the task. In addition, participants correctly withheld their

responses when they detected a facial stimulus (~99%) and this did not differ by emotion (p = .13) or fixation location (p = .17).

4.3.2 ERP Analyses

4.3.2.1 Effects of fixation location and emotion at occipital sites (O1, O2, Oz)

P1 Peak Amplitude. For O1/2, P1 amplitude was larger in the right compared to the left hemisphere (F(1, 25) = 5.29, p < .05, η_p^2 = .18) and overall largest for fixation to the mouth (main effect of fixation, F(2.22, 55.42) = 12.62, p < .0001, η_p^2 = .34) (see Fig. 13A). As seen in Exp. 1, an interaction between fixation location and hemisphere (F(2.33, 58.25) = 19.65, p < .0001, η_p^2 = .44) was due to eye fixations yielding opposite effects on each hemisphere. On the left hemisphere, P1 was larger for the mouth and left eye (which did not differ significantly) compared to the right eye and the nose fixations (which did not differ) (F = 20.32, p < .0001; η_p^2 = .45). On the right hemisphere, P1 was larger for the mouth and right eye (which did not differ significantly) compared to the left eye and nose fixations which did not differ (F = 11.57, p < .001; η_p^2 = .32; significant paired comparisons p < .01). P1 at Oz was also larger for fixation to the mouth compared to all other fixation locations which did not differ significantly from each other (main effect of fixation location, F(2.42, 60.53) = 14.69, p < .0001, η_p^2 = .37; significant paired comparisons with mouth fixation at p < .05) (Fig. 13A).

In contrast to Exp. 1 (GD task) and 2 (ED task), an effect of emotion was found for P1 at O1/2 sites, with reduced positivity for happy compared to neutral (and fearful) faces (main effect of emotion, F(1.89, 47.22) = 4.74, p = .015, η_p^2 = .16; significant paired comparisons happy-neutral p = .024 and happy-fearful p = .05). This emotion effect was also seen at Oz (main effect of emotion, F(1.97, 49.23) = 6.51, p < .01, η_p^2 = .21; Fig 13B), although only for the mouth fixation

(emotion by fixation location interaction at Oz, $F(5.13, 128.30) = 3.86$, $p < .005$, $\eta_p^2 = .13$; effect of emotion at mouth fixation: $F = 16.1$, $p < .001$; significant happy-neutral and happy-fearful paired comparison at $p < .005$; no emotion effect for left eye ($p = .82$), right eye ($p = .59$) or nose ($p = .082$); Fig 13C P1 bar graph). Difference waveforms (fearful-neutral and happy-neutral, across fixation locations) clearly revealed this happy effect at occipital sites that was largest around 120ms (Fig. 13B-C and map). This early effect was confirmed with mean amplitude analyzes during the 100-150ms window (see below).

Table 11. *Exp. 3 (Oddball task) statistical effects on mean amplitudes analyzed over six 50ms time windows at occipital sites (O1, Oz, O2), with F, p and η_p^2 values. LH, left hemisphere; RH, right hemisphere; LE, left eye; RE, right eye; No, nose; Mo, mouth; F, fear; H, happy; N, neutral. Main effects p values: p* < .05; p** < .01; p*** < .001; p**** < .0001; ns, not significant. Bonferroni-corrected significant paired comparison tests (p < .05) are also reported (e.g., H < F + N means that mean amplitude for happy was significantly smaller compared to both fearful and neutral expressions, while H + F < N means that mean amplitudes for both happy and fearful faces were significantly smaller than to neutral expressions).*

Main effects and interactions	50-100ms	100- 150ms	150- 200ms	200-250ms	250-300ms	300-350ms
Electrode	*F* = 4.41, *p** , η_p^2 = .15 O2 > Oz	*F* = 12.71, *p**** , η_p^2 = .34 O1 +O2 > Oz	*F* =4.07 *p** , η_p^2 = .14 No sign. paired comp.	*F* = 12.83, *p*** , η_p^2 = .34 O1 + O2 > Oz	*F* = 29.61, *p*****, η_p^2 = .54 O1 + O2 > Oz	*F* = 15.66, *p*****, η_p^2 = .38 O1 + O2 > Oz
Fixation location	-	*F* = 40.98, *p*****, η_p^2 = .62 Mo > all and LE > RE	*F* = 7.48, *p***, η_p^2 = .23 No > RE + Mo	*F* = 6.67 , *p***, η_p^2 = .21 All > Mo	*F* = 4.55 , *p***, η_p^2 = .15 LE > No	-
Emotion	-	*F* =16.32, *p*****, η_p^2 = .40 H < F + N	*F* = 13.72, *p****, η_p^2 = .35 H + F < N	*F* = 16.65, *p*****, η_p^2 = .40 H + F < N	*F* = 9.50, *p****, η_p^2 = 28 H < N	*F* = 12.46, *p*****, η_p^2 = .33 H + F < N
Electrode X Fixation location	*F* = 10.11, *p****, η_p^2 = .29 • O1: *F* = 4.27, *p**, η_p^2 = .15 LE > RE • O2: *F* =3.83 *p**, η_p^2 = .13 RE > LE + No • Oz: ns	-	*F* = 2.65, *p**, η_p^2 = .1 • O1: *F* = 7.2, *p***, η_p^2 = .22 No > RE + Mo; LE > RE • O2: *F* =7.83 *p***, η_p^2 = .24 No > all • Oz: *F* =4.96 *p**, η_p^2 = .17 No > RE + Mo	-	-	-
Electrode X Emotion	-	*F* = 4.20, *p**, η_p^2 = .14 • O1: *F* = 9.09, *p***, η_p^2 = .27 H < F + N • O2: *F* =15.93, *p*****, η_p^2 = .39 H < F + N • Oz: *F* = 16.91, *p*****, η_p^2 = .40 H < F + N	*F* = 2.77, *p**, η_p^2 = .1 • O1: *F* = 7.0, *p***, η_p^2 = .22 H + F < N • O2: *F* =15.99 *p****, η_p^2 = .39 H + F < N • Oz: *F* =12.54 *p****, η_p^2 = .33 H + F < N	-	-	
Emotion X Fixation location	-	*F* =4.38, *p***, η_p^2 = 15 • Mo: *F* = 21.22, *p*****, η_p^2 = .46 H < F + N • No: *F* = 8.98, *p***, η_p^2 = .26 H < F + N • LE: ns • RE: ns	*F*= 3.22, *p**, η_p^2 = .11 • Mo: *F* = 17.11, *p* *****, η_p^2 = .41 H + F < N • No: *F* = 4.40, *p**, η_p^2 = .15 F < N • LE: ns • RE: ns	-	-	*F*= 3.26, *p**, η_p^2 = .12 • Mo: *F* = 17.43, *p* *****, η_p^2 = .41 F + H < N • No: ns • LE: ns • RE: ns

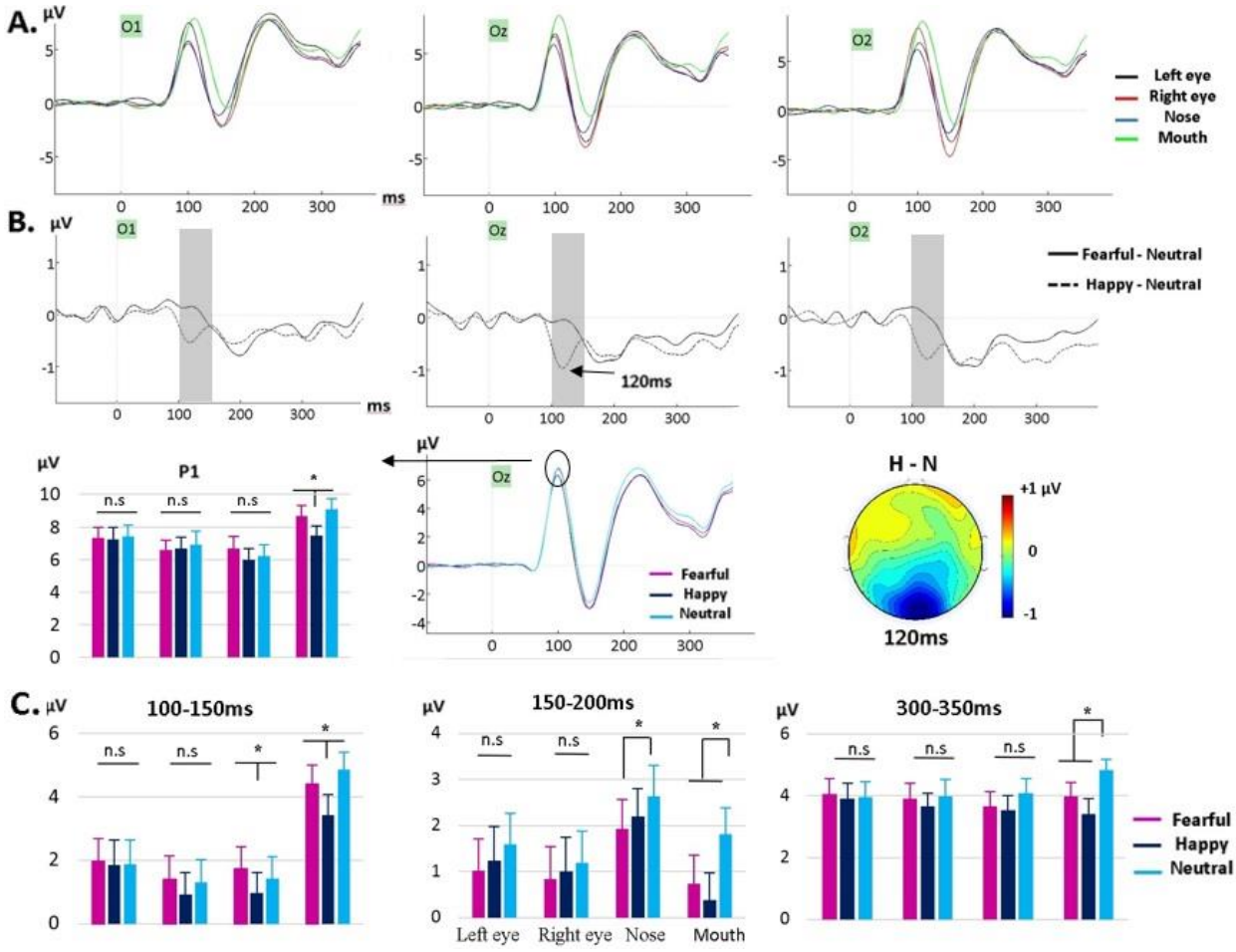


Figure 13. Effects of Fixation Location and Emotion Occipital Sites (Exp.3)

(A) Grand-averages featuring the P1 component for Exp. 3 (ODD) for neutral faces at O1, O2, and Oz electrodes, showing effects of fixations with larger amplitudes for mouth fixation and opposite hemispheric effects for eye fixations. (B) *Top row*: Grand-average difference waveforms generated by subtracting ERPs to neutral from ERPs to fearful faces (F-N, solid line) and ERPs to neutral from ERPs to happy faces (H-N, dashed line) at O1, O2 and Oz (across fixation locations). A clear peak for the happy-neutral difference was seen between 100-150ms (gray band, peak of the effect around 120ms at which the topographic map is shown) and was confirmed by mean amplitude analysis at occipital sites during that time window (see main text and Table 11). *Bottom row*: Grand-averaged waveforms for fearful, happy and neutral faces (across fixation locations) at Oz showing the "happy effect" starting at P1 although only for the mouth fixation condition (left bar graph). (C) Emotion effects were seen only during fixation to the nose and mouth between 100-150ms (bottom left bar graph) and between 150-200ms (bottom middle bar graph); emotion effects were seen only for the mouth fixation during the 300-350ms interval (bottom right bar graph).

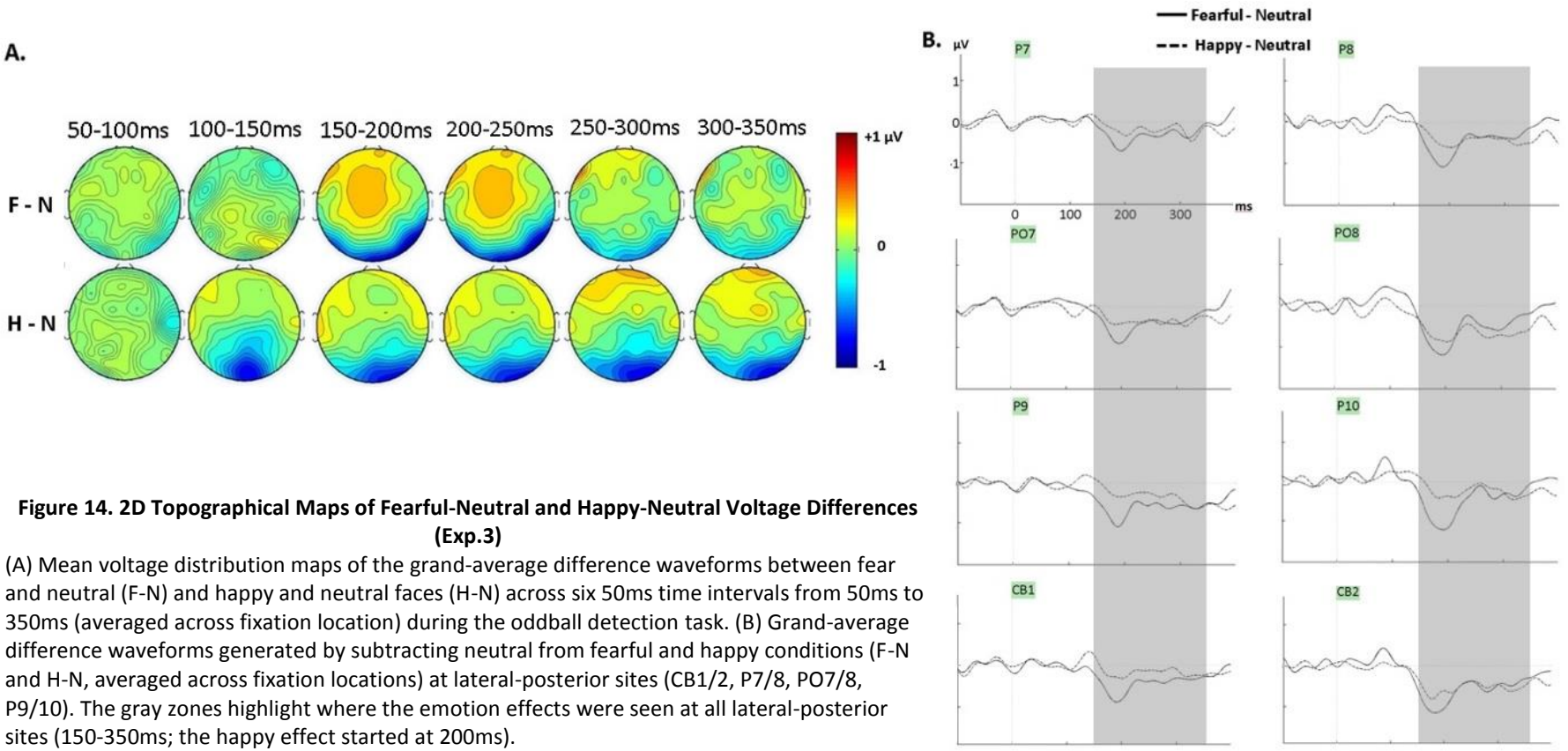


Figure 14. 2D Topographical Maps of Fearful-Neutral and Happy-Neutral Voltage Differences (Exp.3)

(A) Mean voltage distribution maps of the grand-average difference waveforms between fear and neutral (F-N) and happy and neutral faces (H-N) across six 50ms time intervals from 50ms to 350ms (averaged across fixation location) during the oddball detection task. (B) Grand-average difference waveforms generated by subtracting neutral from fearful and happy conditions (F-N and H-N, averaged across fixation locations) at lateral-posterior sites (CB1/2, P7/8, PO7/8, P9/10). The gray zones highlight where the emotion effects were seen at all lateral-posterior sites (150-350ms; the happy effect started at 200ms).

Mean Amplitudes over Six Time Windows (O1, O2, Oz). Statistical results for these analyses (50-350ms) are reported in Table 11 and visually depicted in Figures 13 and 14A.

Between 50 and 100ms, fixation location interacted with electrode such that mean amplitudes at O1 were larger for left eye fixation than right eye fixation while the opposite was found at O2, reflecting a different effect of fixation to the eyes on each hemisphere, as seen on the P1 peak (Table 11, Fig. 13). More positive amplitudes were seen when fixation was on the mouth compared to the other facial features between 100 and 150ms (Fig.13A). From 150 to 300ms various fixation effects were seen (Table 11) with no clear stable pattern.

As seen in Exp.1 and 2, an emotion effect was first seen during the 100-150ms time window with smaller amplitudes for happy compared to neutral (and fearful) expressions (Fig. 13B-C), confirming the main effect found on P1 peak reported previously. However, in contrast to Exp.1 and 2, an emotion by fixation location interaction revealed this effect was seen for the nose and mouth fixation conditions, but not for the eyes fixation conditions (Table 11, Fig.13C, bottom left panel). From 150 to 200ms, both happy and fearful faces elicited smaller amplitudes than neutral faces although again, these effects were seen only for the mouth fixation (Fig.13C, bottom middle panel), as was also seen in Exp.1 and .2. For nose fixation, only the fearful-neutral difference was significant, while no emotion effect was seen when fixation was on the eyes. Between 100 and 200ms, these emotion effects were seen at all occipital sites but were slightly more pronounced at O2 and Oz (electrode by emotion interaction, Table 11). From 200 to 300ms happy expressions continued to elicit smaller amplitudes compared to neutral expressions regardless of fixation location (fear elicited smaller amplitudes than neutral from 200 to 250ms). However, from 300 to 350ms the happy and fearful effects were once again only seen for the

mouth fixation condition (Fig.13C, bottom right panel). Overall, the distribution of the happy and fearful effects over occipital sites was extremely similar to that seen in Exp.1 and Exp.2 (see Fig.14) with additional interactions between fixation location and emotion in 2 time windows.

4.3.2.1 Effects of fixation location and emotion at lateral-posterior sites (CB1/2, P9/10, P7/8, PO7/8)

N170 Peak Amplitude. The N170 amplitude was larger in the right compared to the left hemisphere ($F(1,25) = 7.12$, $p = .013$, $\eta_p^2 = .22$) and for fixation to the left and right eye (which did not differ) compared to fixation to the mouth and nose which did not differ significantly (main effect of fixation location, $F(2.66, 66.41) = 23.52$, $p < .0001$, $\eta_p^2 = .49$; all paired comparisons at p-values < .001) (Fig. 15A). In contrast to Exp.1 the N170 was larger for fearful compared to neutral and happy faces which did not differ (Fig. 15B) (main effect of emotion, $F(1.93, 48.33) = 10.34$, $p < .001$, $\eta_p^2 = .29$; significant fearful-neutral and fearful-happy paired comparisons $p < .01$). There was also an emotion by hemisphere interaction ($F(1.94, 48.37) = 4.33$, $p = .02$, $\eta_p^2 = .15$) such that N170 amplitudes were larger for fearful compared to both neutral and happy faces in the left hemisphere (emotion effect, $F = 11.28$, $p < .001$; significant fearful-neutral paired comparison p =.028 and fearful-happy $p = .001$) however larger for fearful only compared to neutral faces in the right hemisphere ($F = 6.61$, $p < .01$; significant paired comparison $p = .003$).

P1-to-N170 amplitude. Replicating Exp.1 and 2, amplitude differences were larger in the right compared to the left hemisphere (main effect of hemisphere, $F(1, 25) = 14.79$, $p < .001$, $\eta_p^2 = 37$) and were larger during fixation to both the left and right eye (which did not differ) compared to the nose and mouth (which did not differ) (main effect of fixation location, $F(2.32, 57.93) = 37.56$, $p < .0001$, $\eta_p^2 = .60$; significant left eye-nose/mouth and right eye-nose/mouth paired comparisons $p < .0001$). Once again, this confirmed the fixation location effect found for the N170

peak. An interaction between fixation location and hemisphere was also seen (F(2.05, 51.15) = 7.20, p < .01, η_p^2 = .22), due to opposite effects of eye fixation in each hemisphere, driven by the P1 (Fig.15A): on the left hemisphere, amplitude was larger for the left than the right eye (p <.001) while the opposite was seen on the right hemisphere (RE > LE, p =.014).

In line with the emotion effect at the N170, P1-N170 amplitude difference was overall largest for fearful faces (main effect of emotion, F(1.86, 46.60) = 6.40, p < .01, η_p^2 = .20; significant fearful-neutral comparison p = .002), but this effect interacted with hemisphere (F(1.89, 47.40) = 4.92, p=.013, η_p^2 = .16). The analysis of each hemisphere separately confirmed an emotion effect for the right hemisphere (F =8.96, p=.001, η_p^2 = .26), with larger amplitude for fearful than neutral faces, but no emotion effect for the left hemisphere (p =.39). There was also a significant interaction between fixation location and emotion (F(4.09, 102.34) = 4.10, p = .004, η_p^2 = .14). A larger P1-N170 amplitude difference for fearful compared to happy faces was seen when fixation was on the nose (F = 6.50, p = .003; paired comparison p = .003) and for both fearful and happy compared to neutral faces when fixation was on the mouth (F = 7.59, p = .002; significant fearful-neutral paired comparison p = .039 and happy-neutral p =.001). When fixation was on the right eye, (F =3.49, p =.045), amplitude tended to be larger for fearful than happy faces but the comparison did not reach significance (p =.078). No emotion effect was seen when fixation was on the left eye (p =.28). Thus, fearful and happy effects were only seen during mouth fixation between P1 and N170 components (~100-150ms).

Mean Amplitude analyses over Six Time Windows (CB1/2, P7/8, P9/10, PO7/8). Statistical results for these analyses (50-350ms) are reported in Table 12 and visually depicted in Figures 14 and 15.

Between 50 and 100ms, fixation to the eyes had opposite effects on each hemisphere (fixation location x hemisphere interaction), reminiscent of the effect seen at occipital sites during that same time and on the P1. The pattern was less clear between 100 and 150ms, during the transition to the N170 component, but between 150 and 250ms, the mean amplitudes were more negative for the eyes than for the nose and mouth, capturing well the fixation effect reported on the N170. After 200ms no clear fixation effect was seen although amplitudes seemed slightly more positive for mouth fixation than for the other fixation locations (Fig.15A).

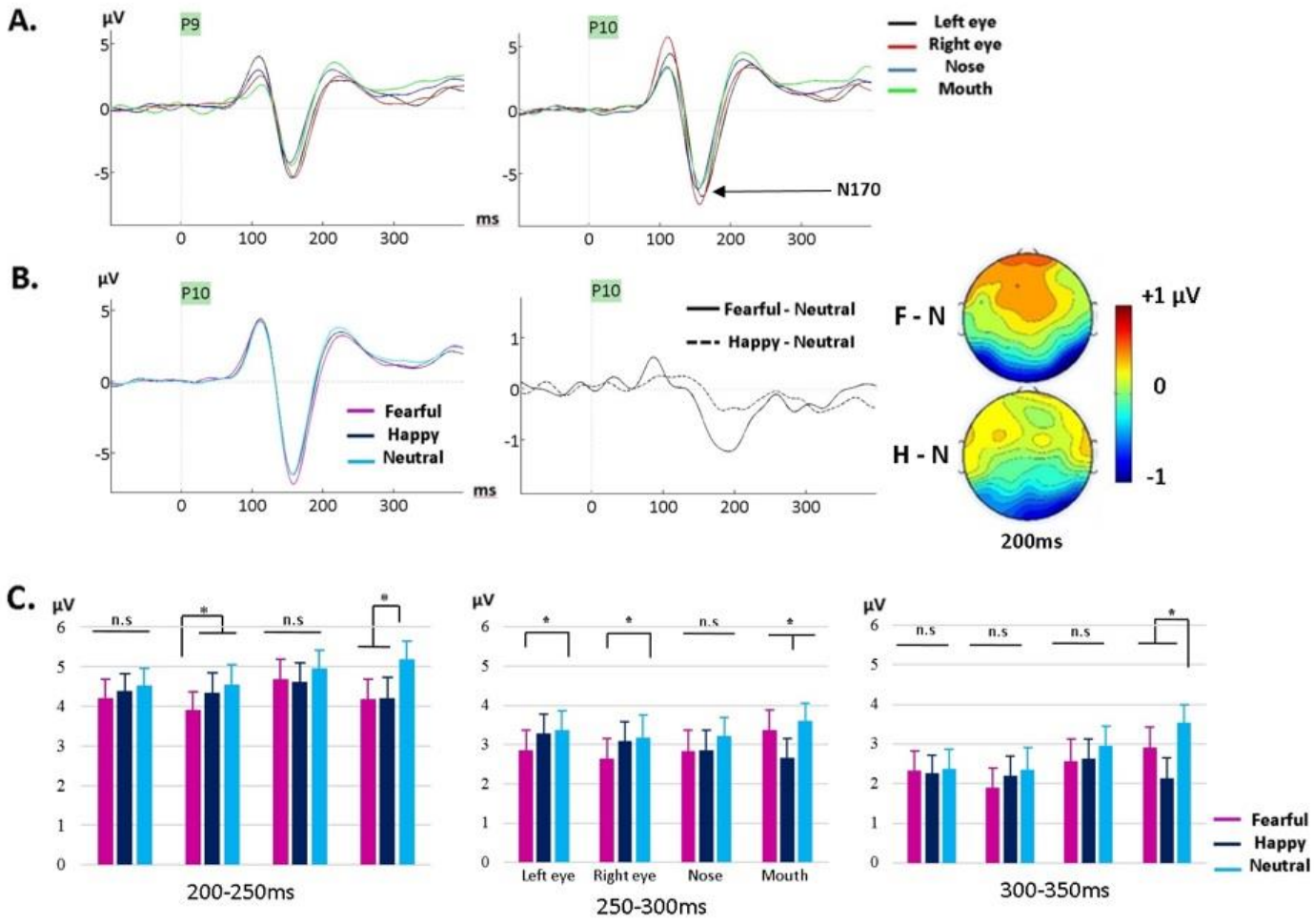


Figure 15. Effect of Fixation Location and Emotion at Lateral-Posterior Sites (Exp.3)

(A) Grand-averages featuring the N170 component for neutral faces at P9 and P10 as a function of fixation location during the oddball detection task. (B) *Left.* Grand-averages for fearful, happy and neutral faces (across fixation locations) at P10 site featuring a larger N170 peak for fearful than neutral and happy faces. *Right.* Grand-average difference waveforms generated by subtracting ERPs to neutral from ERPs to fearful faces (F-N, solid line) and ERPs to neutral from ERPs to happy faces (H-N, dashed line) at P10. The maps show the voltage difference between fearful and neutral faces and between happy and neutral faces, across the scalp at a latency of 200ms where the effects were largest. (C) Emotion by fixation location interactions are displayed in the bar graph: Between 200-250ms (bottom left bar graph) smaller amplitudes for fearful compared to happy and neutral expressions were seen only during fixation to the right eye and smaller amplitudes for both happy and fearful compared to neutral expressions were seen only during fixation to the mouth; between 250-300ms (bottom middle bar graph) smaller amplitudes for fearful compared to neutral expressions were seen during fixation to the left and right eye and smaller amplitudes for happy compared to fearful and neutral expressions during fixation to the mouth; between 300-350ms (bottom right bar graph) smaller amplitudes for fearful and happy expressions compared to neutral were seen only during fixation to the mouth. .

Table 12. *Exp. 3 (ODD) statistical effects on mean amplitudes analyzed over six 50ms time windows at lateral-posterior sites (CB1/2, P7/8, PO7/8, P9/10), with F, p and η_p^2 values. LH, left hemisphere; RH, right hemisphere; LE, left eye; RE, right eye; No, nose; Mo, mouth; F, fear; H, happy; N, neutral. Main effects p values: p* < .05; p** < .01; p*** < .001; p**** < .0001; ns, not significant. Bonferroni-corrected significant paired comparison tests are also reported (e.g., F < H + N means that mean amplitudes for fearful faces were significantly smaller compared to both happy and neutral expressions, while F + H < N means that mean amplitudes for both fearful and happy faces were significantly smaller than to neutral expressions).*

Main effects and interactions	50-100ms	100- 150ms	150- 200ms	200-250ms	250-300ms	300-350ms
Electrode	*F* = 28.78, *p*****, η_p^2 = .54 P9/10 < CB1/2 + P7/8 < PO7/8	*F* = 25.60, *p*****, η_p^2 = .45 P9/10 < CB1/2 + P7/8 < PO7/8	*F* =31.9, *p*****, η_p^2 = .56 P9/10 < CB1/2 + P7/8 < PO7/8	*F* = 52.48, *p*****, η_p^2 = .68 P9/10 < CB1/2 + P7/8 < P7/8 < PO7/8	*F* = 46.77, *p*****, η_p^2 = .65 P9/10 + CB1/2 < P7/8 < PO7/8	*F* = 42.01, *p*****, η_p^2 = .63 P9/10 + CB1/2 < P7/8 < PO7/8
Hemisphere	*F* = 5.59, *p**, η_p^2 = .18 RH > LH	-	*F* = 5.54, *p**, η_p^2 = .18 RH < LH	*F* = 13.02, *p***, η_p^2 = .34 RH > LH	*F* = 16.84, *p****, η_p^2 = .40 RH > LH	*F* = 5.24, *p**, η_p^2 = .17 RH > LH
Fixation location	-	*F* = 8.82, *p****, η_p^2 = .26 LE + Mo > No	*F* = 32.00, *p*****, η_p^2 = .56 LE + RE < Mo < No	*F* = 4.12, *p**, η_p^2 = .14 No > RE	-	*F* = 6.54, *p***, η_p^2 = .21 Mo > RE
Emotion	*F* = 3.53, *p**, η_p^2 = .12 H < F	-	*F* = 18.34, *p*****, η_p^2 = .42 F < H < N	*F* = 15.44, *p*****, η_p^2 = .38 F + H < N	*F* = 7.97, *p***, η_p^2 = .24 F + H < N	*F* = 11.02, *p***, η_p^2 = .31 F + H < N
Emotion X Electrode	-	*F* = 5.60, *p***, η_p^2 = 18 • P9/10:*F* = 5.30, *p***, η_p^2 = .18 F < H • P7/8: ns • PO7/PO8: ns • CB: ns	*F* = 2.96, *p**, η_p^2 = 11 • P9/10: *F*=24.7, *p*****, η_p^2 = .5 F < H + N • P7/8: *F*=10.78, *p****, η_p^2 = .3; F < H + N • PO7/P8: *F*=11.63, *p****, η_p^2 = .32 F + H < N • CB: *F* =13.9, p***, η_p^2 = .36 F < H + N			
Hemisphere X Fixation location	*F* = 10.45, *p****, η_p^2 = .30 • LH: *F* = 4.71, *p***, η_p^2 = .16 LE > RE • RH: *F* = 5.46, *p***, η_p^2 = .18 RE > LE + Mo	*F* =4.77, *p***, η_p^2 = 16 • LH: *F* =3.28, *p**, η_p^2 = .12 LE > No • RH: *F* =6.33, *p* **, η_p^2 = .20 LE + RE + Mo > No	-		*F* =4.13, *p**, η_p^2 = 14 • LH: *F* =6.47, *p*8, η_p^2 = .21 RE < LE + Mo • RH: ns	-
Hemisphere X Emotion	-	-	*F* = 5.04, *p**, η_p^2 = .17 • LH: *F* =11.18, *p****, η_p^2 = .31 F < H + N • RH: *F* =19.23, *p*****, η_p^2 = .44 F < H < N	*F* = 3.83, *p**, η_p^2 = .13 • LH: *F* =10.3, *p****, η_p^2 = .29; F < H + N • RH: *F* =15.65, *p*****, η_p^2 = .39 F + H < N	*F* = 3.4, *p**, η_p^2 = .12 • LH: *F* =5.5, *p***, η_p^2 = .18 F < N • RH: *F* =8.33, *p****, η_p^2 = .25 F + H < N	
Emotion X Fixation location	*F* = 3.67, *p***, η_p^2 = .13 • LE: ns • RE: ns • No: *F* = 8.43, *p***, η_p^2 = .25 H < F • Mo: *F* = 3.8, *p**, η_p^2 = .13 Pairwise comparisons ns	-	-	*F* = 3.42, *p**, η_p^2 = .12 • LE: ns • RE: *F* = 5.72, *p***, η_p^2 = .19 F < H + N • No: ns • Mo: *F* = 15.79, *p*****, η_p^2 = .39 F + H < N	*F* = 5.15, *p***, η_p^2 = .17 • LE: *F* = 4.44, *p**, η_p^2 = .15 F < N • RE: : *F* = 4.34, *p**, η_p^2 = .15 F < N • No: ns • Mo: *F* = 11.78, *p***, η_p^2 = .32 H < F + N	*F* =5.95, *p****, η_p^2 = .19 • LE: ns • RE: ns • No: ns • Mo: *F* = 25.91, *p*****, η_p^2 = .51 H < F < N

Small amplitude differences were seen between happy and fearful expressions between 50 and 100ms as an interaction with fixation location, and between 100 and 150ms at one electrode pair only (Table 12). However, as no difference was seen between any emotion and neutral expressions, these sporadic effects are treated as meaningless. A true fear effect was seen at all lateral-posterior electrodes from 150 to 350ms, with smaller amplitudes for fearful than neutral expressions, best captured by difference waves as a sustained bilateral negativity (Fig. 14-15). A similar, albeit much weaker, happy effect was also seen during that time period, with smaller amplitudes for happy than neutral faces. From 200ms until 350ms these emotion effects interacted with fixation location (Table 12, Fig.15C). The fear effect was seen for fixation on the right eye between 200-300ms, for fixation on the left eye between 250 and 300ms, and for fixation on the mouth between 200-250ms and 300-350ms. The happy effect was seen only during the mouth fixation condition. No effect of emotion was seen when fixation was on the nose.

4.4 Discussion

Using the same gaze-contingent procedure as Exp.1 and 2, I investigated the effects of fixation to different facial features on the neural processing of fearful, happy and neutral facial expressions during an oddball detection task. While this task required less attention to the face compared to the gender and emotion discrimination tasks, overall behavioural performance was excellent demonstrating that participants were in fact attending to the task.

Consistent with Exp. 1 and 2, P1 and N170 peaks, as well as the P1-to-N170 amplitude difference, were sensitive to fixation location. Fixation effects on the P1 reflected differences in face position on the screen (Fig.1) whereas effects on the N170 reflected an eye sensitivity during

encoding of the structure of the face (Nemrodov et al., 2014). These effects were discussed in greater detail in chapter 2 (section 2.4.2).

Emotion effects were also consistent with Exp.'s 1 and 2, providing a second replication for distinct effects with different distributions for fearful and happy expressions. An early happy effect began ~100ms and lasted until 350ms at occipital sites (weakly at lateral-posterior sites), and the fearful effect was seen at ~150ms and lasted until 350ms at lateral-posterior sites (weakly at occipital sites). Despite no modulation of the N170 by emotion in Exp. 1 and 2, the N170 amplitude was larger for fearful compared to neutral (and happy) expressions in Exp. 3. Inspection of the difference waves and topographical maps (Figures 4, 6, 9, and 14) revealed that the fear effect was extremely similar between the three experiments. It started around or right after the N170 and continued until 350ms, encompassing the so-called Early Posterior Negativity – EPN (Leppänen et al., 2008; Rellecke et al., 2013; Schupps et al., 2004; see Hinojosa, Mercado, & Carrietié, 2015). The reason why this effect starts slightly earlier in some studies (e.g., in the present ODD task) so as to impact the N170, but not in other studies (e.g., the gender task in Exp.1 and explicit task in Exp.2) remains unknown, but could be related to attentional task demands (Hinojosa, Mercado, & Carrietié, 2015). The present study cannot directly address this issue with sufficient statistical power, given that different participants were administered the GD, ED and ODD tasks. Again, as in the previous two studies, there was no early effect for fear on the P1. Previous reports of early fear effects in oddball detection tasks (e.g., Batty & Taylor, 2003; Williams et al., 2004) therefore may have been driven by low-level stimulus properties which were not controlled for.

This was the first study to test the impact of fixation to facial features on the neural response to facial expressions during an oddball detection task and whether or not an interaction between emotion and fixation location would be seen was difficult to predict. Results revealed that the emotion effects for happy and fearful expressions did in fact interact with fixation to facial features. The early and later happy effect seen mostly at occipital sites (and to a lesser extent at lateral-posterior sites) interacted with fixation to mouth such that processing of happy expressions was seen only during fixation to the mouth between 100-200ms and 200-350ms at occipital sites and between 200 and 350ms at lateral-posterior sites. This early effect for happy expressions seen in early visual areas likely via the fast discrimination of the diagnostic smile (based on low-level characteristics as proposed by Halgren et al., 2000) occurs in tasks requiring various degrees of attention to the face. Information from the mouth also appears to be important for processing of the emotional content of the face as evidenced by interactions seen at lateral-posterior sites later during the timing of the EPN.

The fear effect interacted with fixation to the mouth beginning at 150-200ms at occipital sites and at lateral-posterior sites between 200 and 300ms. The fear effect was also seen during fixation to the eyes between 200 and 250ms. Thus information provided by the mouth and the eyes appears to be critical for processing of the emotional content of fearful expressions even when attention is not directed to the emotional content of the face, and also during emotion categorization tasks (Exp.2). This is in line with visual scanning studies where participants spent most time fixating on both eyes and the mouth of fearful faces (Eisenbarth & Alpers, 2011). The reason why the fear effect interacted with fixation to facial features in Exp.2 (GD) and Exp.3 (ODD) but not in Exp.1 (GD) remains unclear and will be discussed in the general discussion.

Chapter 5: Impact of task demands on the neural processing of fearful and happy expressions

5.1 Introduction

The current literature regarding the time course of facial expression processing is inconsistent (Vuilleumier & Pourois, 2007). While it is commonly acknowledged that an enhanced negative-going potential for emotional expressions relative to neutral expressions is seen over posterior-lateral scalp electrodes, beginning as early as 150ms and largest between 200 and 350ms (the early posterior negativity –EPN; e.g., Rellecke et al., 2011; Schupp et al., 2004), the sensitivity of the preceding P1 and face-sensitive N170 components to facial expressions remains debated. A possible explanation for the inconsistency in reported early emotional effects is the fact that various experimental tasks have been used during the ERP recording of emotional faces. A variety of emotion-relevant and emotion-irrelevant tasks have been employed including face vs. non-face judgments (oddball detection tasks, Batty & Taylor, 2003; Leppänen et al., 2007; Williams et al., 2004; Present thesis Exp.3), pure passive viewing of emotional faces (Blau et al., 2007; Hermann et al., 2002; Pizzagalli et al., 2002; Schupp et al., 2004; Smith et al., 2013), categorization of face gender (gender discrimination, Pourtois et al., 2005; Sato et al., 2001; Wijers & Banis, 2014; Present thesis Exp.1) and categorization of facial emotion (explicit emotion discrimination, e.g., Eimer et al., 2003; Calvo & Beltrán, 2014; Leppänen et al., 2008; Schacht & Sommer, 2009; Present thesis Exp.2). The differences in attention directed to the face placed by these various task demands may impact the processing of facial emotions differently.

The debated P1 modulation for fearful compared to neutral and happy faces has been most commonly reported in studies using tasks where emotion was irrelevant including oddball

detection tasks (e.g., Batty and Taylor, 2003; Williams et al., 2004) and passive viewing of emotional faces (e.g., Pizzagalli et al., 2002). This, together with reports of increased amygdala activation to fearful faces during emotion-irrelevant tasks, has led authors to suggest the automatic (i.e., involuntarily) and rapid detection of salient threatening fearful faces via a subcortical route involving the amygdala (see Palermo & Rhodes, 2007 for a review). If this is true, this early effect for fearful expressions would be seen only when attention is directed away from the emotional content of the face and therefore not in explicit emotion discrimination tasks; however, this has not been directly tested.

The relationship between task and emotion effects reported on the face-sensitive N170 are less clear. Early effects have been reported for fearful compared to neutral and happy faces during emotion-irrelevant (Batty & Taylor, 2003; Blau et al., 2007; Leppänen et al., 2007) and emotion-relevant tasks (e.g., Calvo & Beltrán, 2014; Leppänen et al., 2008; Morel et al., 2014). Additionally, a lack of sensitivity of the N170 to fearful expressions (compared to neutral expressions) has also been reported in both emotion-irrelevant tasks (Hermann et al., 2002; Meaux et al., 2014; Schupp et al., 2004; Smith et al., 2013; and see Vuilleumier & Pourtois, 2007 and Rellecke et al., 2013) and emotion-relevant tasks (e.g., Eimer et al., 2003; Leppänen et al., 2007). The current literature suggests that experimental procedure, including the type of reference used in the EEG montage (e.g., Rellecke et al., 2013), and possibly task demands (Hinojosa, Mercado, & Carrietié, 2015), may partly explain the inconsistent effects reported; however, experiments directly testing whether or not task impacts the early neural response to facial expressions is lacking.

In the current series of studies (Exp.'s 1 to 3), where task varied between experiments, results support the idea that the neural response to fearful and happy expressions may be impacted by task demands. Effects seen for fearful faces (compared to neutral faces) showed some variations between tasks. An early effect for fear ~80ms (*before* the P1) localized to left hemisphere electrodes PO7 and P7 was seen only in Exp. 1 (GD). The added negativity for fearful faces at lateral-posterior sites emerged *after* the N170 in Exp. 1 (GD) and Exp. 2 (ED), while it was seen on the N170 peak itself in Exp. 3 (ODD). Additionally, this fear effect was not seen on the nose fixation during Exp.2 (ED) and Exp.3 (ODD) between ~250-350ms, however, occurred irrespective of fixation location in Exp.1. For happy faces, effects were seen at occipital sites emerging ~100ms with a first local peak around 115-120ms post-stimulus; however, the strength of this happy effect seemed to vary between studies. An effect was seen clearly on the P1 at lateral occipital electrodes in Exp.3 (ODD) but was localized at medial occipital site Oz in Exp.1 (GD) and 2 (ED). Overall the distribution of the fearful and happy effects looked similar between tasks, but some differences in the timing of these effects were found between experiments that could be related to the task demands and the goal of the current study was to test this directly.

The literature reviewed above, derived from many experiments with different subjects and methodology, together with the differences reported between the current series of studies using different tasks, suggests a possible influence of task demands. However, to test for the role of task demands with adequate statistical power, task needs to be tested within-subjects. A few neuroimaging studies have directly compared implicit and explicit tasks using facial expressions and found different activation patterns depending on the task (Lange et al., 2003; Straube et al., 2004). Amygdala and inferior occipital gyrus activations were stronger during emotion-irrelevant

compared to emotion-relevant tasks for fearful compared to neutral faces (Lange et al., 2003). Straube et al. (2004) reported larger amygdala activation for angry faces during an implicit compared to an explicit emotion task, suggesting brain responses to threatening angry faces are most pronounced when facial expression is task-irrelevant. To the best of my knowledge there are at present only two ERP studies that have directly investigated the impact of task demands on the early neural response to facial expressions in a within-subject design. The first was a study by Wronka and Walentowska (2011). In this study participants were asked to categorize angry, happy and neutral expressions as either emotional or neutral during an emotion discrimination task and to categorize face gender in a separate task. Mean N170 amplitude (measured across a 140-185ms window) was larger for emotional faces compared to neutral faces during the emotion discrimination task but not during the gender discrimination task. In contrast, an enhanced negativity (i.e., the EPN) measured between 240-340ms was seen for emotional compared to neutral faces during both tasks. Results suggested that voluntary attention to the expressions can influence face emotion processing ~140-185ms (encompassing the N170) whereas involuntary and mandatory differentiation of facial expression is seen later ~240-340ms. The second study by Rellecke et al. (2012) presented participants with angry, happy and neutral expressions while asking them to either passively view the faces, discriminate faces from words, identify face gender and explicitly identify the emotional expressions (four different tasks tested). Angry expressions elicited larger P1 and N170 amplitudes than neutral faces in both emotion-relevant and emotion –irrelevant tasks while an increased response to happy expressions compared to neutral was seen only at a later time windows (200-600ms) during the gender and emotion discrimination tasks. These results suggested deep processing of threat-related (angry)

expressions regardless of task demands whereas processing of happy expressions requires attention to process the stimuli at a deeper level (Rellecke et al., 2012). Although somewhat contradictory, these two studies provide further support for the idea that task-related factors affect the timing of brain responses to angry and happy expressions. However, the impact of task demands on processing of fearful expressions remains to be tested.

Using eye-tracking to ensure fixation to the portion of the face desired, the current study tested the impact of task demands on the neural processing of fearful and happy expressions. Fixation location was not manipulated in this study. Instead, a central fixation landing on the tip of the nose (where holistic processing is most efficient) was used. This central location is also what has been used in most previous research on facial expressions (either tip of nose or nasion – in between the two eyes). Fearful, happy, and neutral expressions were presented in three task conditions: (1) Gender discrimination requiring categorization of face gender (GD), (2) Emotion Discrimination requiring categorization of the facial expression (ED) and (3) Oddball detection where participants responded to infrequently presented flower stimuli (ODD). If task demands influenced the neural response to fearful and happy expressions, I expected task by emotion interactions; however, it was also possible that these emotional responses would be observed to the same extent in all tasks; in this instance main effects of emotion would emerge, but no emotion by task interactions.

5.2 Methods

5.2.1 Participants

Fifty-two undergraduate students from the University of Waterloo (UW) were tested and received course credit for their participation. They all lived in North America for at least 10 years

and reported normal or corrected-to-normal vision, no history of head-injury or neurological disease, and were not taking any medication. They all signed informed written consent and the study was approved by the Research Ethics Board at UW. Twenty-three participants were rejected: four due to high anxiety scores (see procedure below), three due to completion of less than half of the study, three due to too many artefacts resulting in too few trials per condition, nine due to too few trials after removing trials with eye movements (see procedure section below), one due to problems recording the EEG file and three due to failure to calibrate participants' eye movements with the eye-tracker. The results from twenty-nine participants were retained for the final analysis (20.4 ± 1.8 years, 15 male, 26 right-handed).

5.2.2 Stimuli

Stimuli consisted of fearful, happy and neutral facial expressions of 8 males and 8 females from the MacBrain Face Stimulus Sett[11] (Tottenham et al., 2009) and 6 flower stimuli. A mirror version of each face was also included, made using Matlab (MathWorks, Inc.), to control for any minor differences in low-level contrast and pixel intensity between the left and right sides. All images were converted to grayscale and an elliptical mask was applied in Adobe™ Photoshop CS5. The faces subtended 6.20° horizontally and 10.52° vertically when viewed from a distance of 70cm and were presented on a gray background for an image visual angle of 9.17° horizontally and 13.57° vertically. The pictures were presented over a white monitor background. Root mean square (RMS) contrast and pixel intensity (PI) of the pictures were calculated using custom

[11] The models used in the present study were models # 2, 3, 6, 8, 20, 24, 33, 34 (used in Exp.'s 1to 3) and 5, 7, 15, 16, 21, 23, 27, 32 (Exp. 4 only)

Matlab (Mathworks, Inc) scripts (see Table 13). Paired t-tests (two-tailed) revealed no differences between emotions (p > .05 for all comparisons) for mean PI and RMS contrast.

Table 13. *Mean pixel intensity and RMS contrast values for the fearful, happy and neutral expressions used in Exp. 4 (standard errors to the means in parenthesis).*

	Mean RMS Contrast (std. error)	Mean Pixel Intensity (std. error)
	Full face	Full face
Fearful	.616 (.002)	.372 (.010)
Happy	.616 (.003)	.371 (.013)
Neutral	.616 (.002)	.368 (.011)

Participants had to fixate on the tip of the nose. In order to achieve this, the coordinates of the fixation location corresponding to the tip of the nose for each identity and expression was calculated, with minor variations between the 16 identities and the three expressions used.

5.2.3 Apparatus and Procedure

Participants sat in a sound-attenuated Faraday-cage protected booth 70cm from a ViewSonic G225f 21-inch colour monitor driven by an Intel Core I i7-3820 with a refresh rate of 85Hz. Task conditions were presented in separate experimental blocks and the order of the tasks (oddball-detection (ODD), emotion discrimination (ED) and gender discrimination (GD)) was counterbalanced across participants. Task instructions were identical to those administered in Exp.'s 1 to 3 of the thesis: in the ED task, participants had to select the emotion (fear, happy or neutral) from a vertically-presented forced-choice response screen (emotion order counterbalanced across participants) by clicking on the correct label using a computer mouse; in the ODD task participants were told to press the space-bar for flower stimuli; and in the GD task

they discriminated between male and female faces by pressing one of two buttons on a game controller.

Each trial began with a 12-106ms jittered fixation-cross (Figure 16). Participants were instructed to fixate on the black fixation-cross in the center of the screen in order to initiate each trial and keep their eyes fixated there until the response screen appeared. To ensure that participants were fixated on the cross, a fixation contingent trigger enforced the fixation on the cross for 306ms[12]. The target face (or flower in ODD) was then presented for 259ms. In the ODD and GD tasks, the target stimulus was immediately followed by a fixation cross that was presented for 2000ms. This timing was chosen to keep the trial duration time consistent between the three tasks and was in line with previous studies comparing tasks that reported ~2000ms for responses (e.g., Rellecke et al., 2012; Wronka & Walentowski, 2011). In the ED task, the target stimulus was immediately followed by the response screen that was presented until the response.

A block consisted of 96 face trials (3 emotions X 16 identities X 2 standard and mirror-reversed) and for the ODD task each block also contained 12 flowers. Each block was repeated three times with a different trial order (randomized), for a total of 96 trials per face condition. As in the previous experiments, practice trials were given before each task and following the computer task, participants completed the 21- item trait test from the STICSA anxiety scale (Ree, French, MacLeod, & Locke, 2008); only participants scoring in the normal range, below 43 were kept in the analyses (Van Dam, Gros, Earlywine, & Antony, 2013).

[12] Due to sensitivity of the eye-tracker, on average participants took 864.07ms (909.22S.D) between the onset of the fixation-cross and the stimulus presentation.

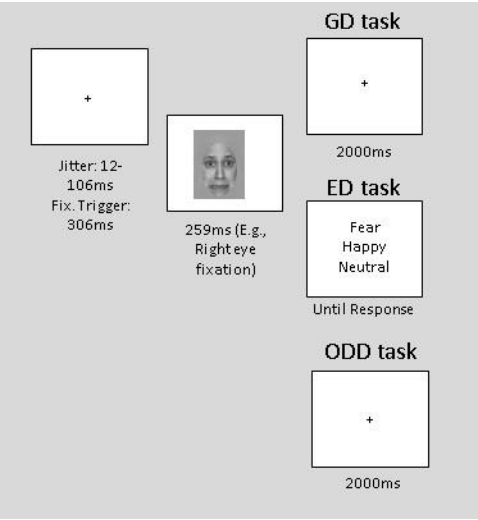


Figure 16. Trial Sequence in the Task Comparison Study (Exp.4)

Participants were tested on 900 trials as follows. First the fixation cross was displayed on the screen for a jittered amount of time (12-106ms) with a fixation trigger of 306ms. Then the grayscale picture was flashed for 259ms, immediately followed by a response screen. During the ODD and GD tasks a white screen with a fixation point appeared for 2000ms during which participants indicated their response. For the ED task the response screen remained until participants made their response.

5.2.3 Electrophysiological recordings

Identical to Exp.'s 1 to 3 (cf. section 2.2.4 pg.21-22), except that the EEG recordings were collected continuously at a 1024Hz sampling rate (instead of 516Hz).

5.2.4 Eye-Tracking Recordings

Identical to Exp.'s 1 to 3 (cf. section 2.2.5 pg.22).

5.2.5 Data Processing and Analyses

Identical to Exp.'s 1 to 3 (cf. section 2.2.6 pg.22-23). For all tasks, only correctly answered trials were used for analysis. Each trial was categorized as correct or incorrect based on the emotion categorization, gender categorization or the detection of flowers. Correct trials were submitted to an outlier detection procedure whereby only trials with RTs within 2.5 standard deviations from the mean of each condition for each subject were retained (Van Selst & Jolicoeur,

1994). This procedure (designed to exclude anticipatory or very long RTs) excluded 6.6% of the total number of trials (across the 29 participants). As in Exp.'s 1-3, trials in which a saccadic eye movement was recorded beyond 1.4° visual angle (70px) around the fixation-location (here the tip of the nose) were removed from further analysis. An average of 2.9% of trials were removed during this step across the 29 participants included in the final sample. After eye movements and artifact-contaminated trial rejection, participants with less than 30 trials in any condition (out of 96 initial trials) were rejected (the average number of trials per condition did not significantly differ across emotions (p = .68) (see Appendix A4 for the final number of trials per condition).

The P1 and N170 components were measured the same way as in Exp.'s 1-3 (P1 at O1, O2, Oz and N170 at the electrode at which it was maximal for each subject, see Table 14). Mean amplitudes at occipital and lateral-posterior sites were also calculated between 50ms and 350ms. ANOVAs were conducted using facial expression (3: fear, happiness, neutral), task (3: ODD, ED, GD), electrode (2 for P1, 3 for mean amplitude at occipital sites, 4 for mean amplitudes at lateral-posterior sites) and hemisphere (2) as within-subject factors. All ANOVAs used Greenhouse-Geisser adjusted degrees of freedom and pairwise comparisons used Bonferroni corrections for multiple comparisons.

Table 14. *Number of subjects for whom the N170 was maximal at left (P9, CB1, PO7) and right (P10, CB2, PO8) hemisphere electrodes. LH: left hemisphere; RH: right hemisphere*

	LH		RH
P9	16	P10	20
CB1	11	CB2	8
PO7	2	PO8	1
Total n	29		29

5.3 Results

5.3.1 Behavioural Analyses.

Gender Discrimination Task (GD). The number of errors (p = .91) and response times (p = .08) did not differ significantly by emotion (Table 15). There were also no differences for miss rates (i.e., no response).

Table 15. *Mean (A) percent error in gender discrimination (responding male to a female face and vice versa), (B) mean reaction times (RT) and (C) mean misses for fearful, happy and neutral expressions presented during the gender discrimination task (standard errors in parenthesis).*

	Mean Error (%) (std.error)	Mean Reaction Time (RT) (ms) (std. error)	Mean Misses (%) (std. error)
Fearful	3.23 (.01)	699.22 (19.63)	.33 (.00)
Happy	3.11 (.01)	686.41 (18.17)	.37 (.00)
Neutral	3.11 (.01)	687.06 (20.16)	.41 (.00)

Emotion Discrimination Task (ED). The overall categorization rate was very good (≥ 80%, Table 16). Overall, participants correctly categorized happy better compared to fearful and neutral faces (main effect of emotion, $F(1.45, 40.72) = 5.00$, $p < .05$, $\eta_p^2 = .15$; significant paired comparisons for happy-fearful $p < .01$ and happy-neutral $p < .05$).

Table 16. *Mean correct categorization responses for fearful, happy and neutral expressions presented during the emotion discrimination task in Exp. 4 (standard errors in parenthesis).*

	Mean (%) Correct (std. error)
Fearful	95.28 (.01)
Happy	99.08 (.00)
Neutral	96.70 (.01)

Oddball Detection Task (ODD). Overall detection of flower stimuli was excellent (~99%) demonstrating that the participants were attending to the task. In addition, participants correctly withheld their responses when they detected a facial stimulus (~99%, Table 17) and this did not differ by emotion (p = .44).

Table 17. *Mean correct rejection (withheld responses) to fearful, happy and neutral expressions presented during the oddball detection task in Exp. 4 (standard errors in parenthesis).*

	Mean (%) Correct (std. error)
Fearful	99.69 (.00)
Happy	99.70 (.00)
Neutral	99.85 (.00)

5.3.2 ERP Analyses

5.3.2.1 Effects of task and emotion at occipital sites (O1, O2, Oz).

P1 Peak Amplitude. No effects were found for P1 analyzed at O1 and O2, or at Oz.

Mean Amplitudes over Six Time Windows (O1, O2, Oz). Statistical results for these analyses (50-350ms) are reported in Table 18 and visually depicted in Figures 17 and 18.

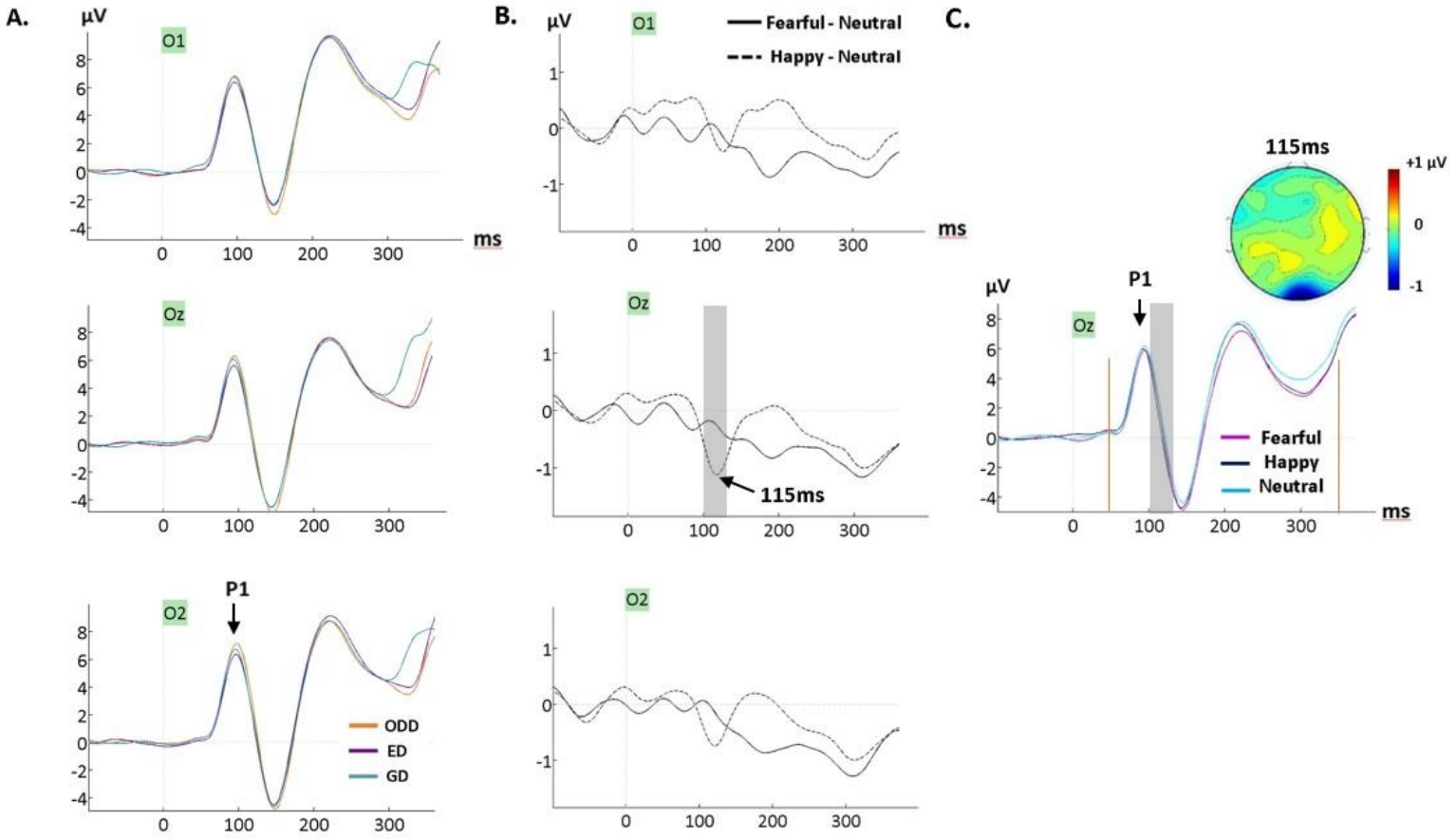


Figure 17. Effects of Task and Emotion at Occipital Sites (Exp.4)

(A) Grand-averages for the three tasks (across emotions) at O1, O2, and Oz electrodes, showing effects of task between 300-350ms with smaller amplitudes for ED and ODD tasks compared to GD task. (B) Grand-average difference waveforms generated by subtracting ERPs to neutral from ERPs to fearful faces (F-N, solid line) and ERPs to neutral from ERPs to happy faces (H-N, dashed line) at O1, O2 and Oz. A clear difference peak for happy-neutral was seen between 110-120ms at Oz and O2 (gray band, peak of the effect around 115ms). (C) Grand-averaged waveforms for fearful, happy and neutral faces (across tasks) at Oz. The early effect of emotion for happy faces started after the P1 peak at Oz. The gray interval (110-120ms) is where the effect emerged, peaking at 115ms. The orange vertical lines represent the limits of the period during which mean amplitudes were analyzed (50-350ms).The topographic map shows the voltage distribution of the H-N amplitude difference at 115ms where the "happy effect" was maximal at medial occipital electrode Oz.

Task demands modulated amplitudes at occipital sites only during the 300-350ms window (Table 18, Fig.17A), with smaller amplitudes for oddball and explicit emotion discrimination tasks compared to the gender task.

A significant effect of emotion was first seen during the 150-200ms time window with smaller amplitudes for fearful compared to neutral (and happy) expressions (Table 18). Although the happy-neutral comparison was not significant in this time window, the happy-neutral difference waveform and the topographic map (Fig. 17B and Fig.18) clearly showed an effect for happy faces localized to medial occipital site ~115ms. Given the similar happy effect found in Exp.'s 1-3 of the thesis, mean amplitudes were further analyzed between 110 and 120ms at Oz, confirming this extremely localized effect with reduced amplitudes for happy faces compared to neutral and fearful faces (main effect of emotion at Oz[13]; $F(1.87, 52.35) = 4.60$, $p = .016$, $\eta_p^2 = .14$; paired comparisons for happy-neutral at $p = .07$ and happy-fearful at $p < .05$). During the 200-250ms and 250-300ms intervals, smaller amplitudes were seen for fearful compared to neutral expressions only. Between 300 and 350ms, both fearful and happy expressions elicited smaller amplitudes compared to neutral expressions.

To summarize, a fearful effect was seen at occipital sites from 150 until 350ms, as clearly seen on the difference waveforms (Fig. 17B). In contrast, a marginal happy effect was seen between 110 and 120ms localized to medial occipital site Oz, and then later on between 300 and 350ms. Importantly, emotion never interacted with task in any time window.

[13] Note that an effect of emotion was also there when all three occipital electrodes were analyzed together ($F=3.32$, $p=.05$) but paired comparisons did not reach significance

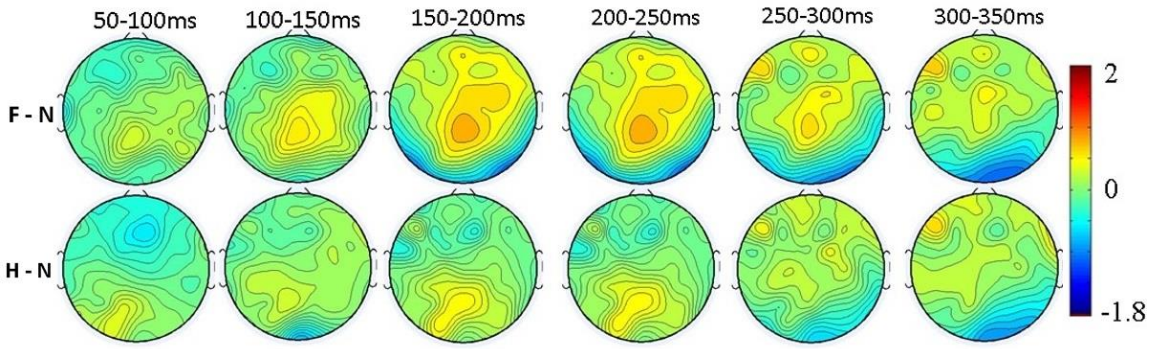


Figure 18. 2D Topographical Maps of Fearful-Neutral and Happy-Neutral Voltage Differences (Exp.4)
Mean voltage distribution maps of the grand-average difference waveforms between fear and neutral (F-N) and happy and neutral faces (H-N) across six 50ms time intervals from 50ms to 350ms (averaged across tasks).

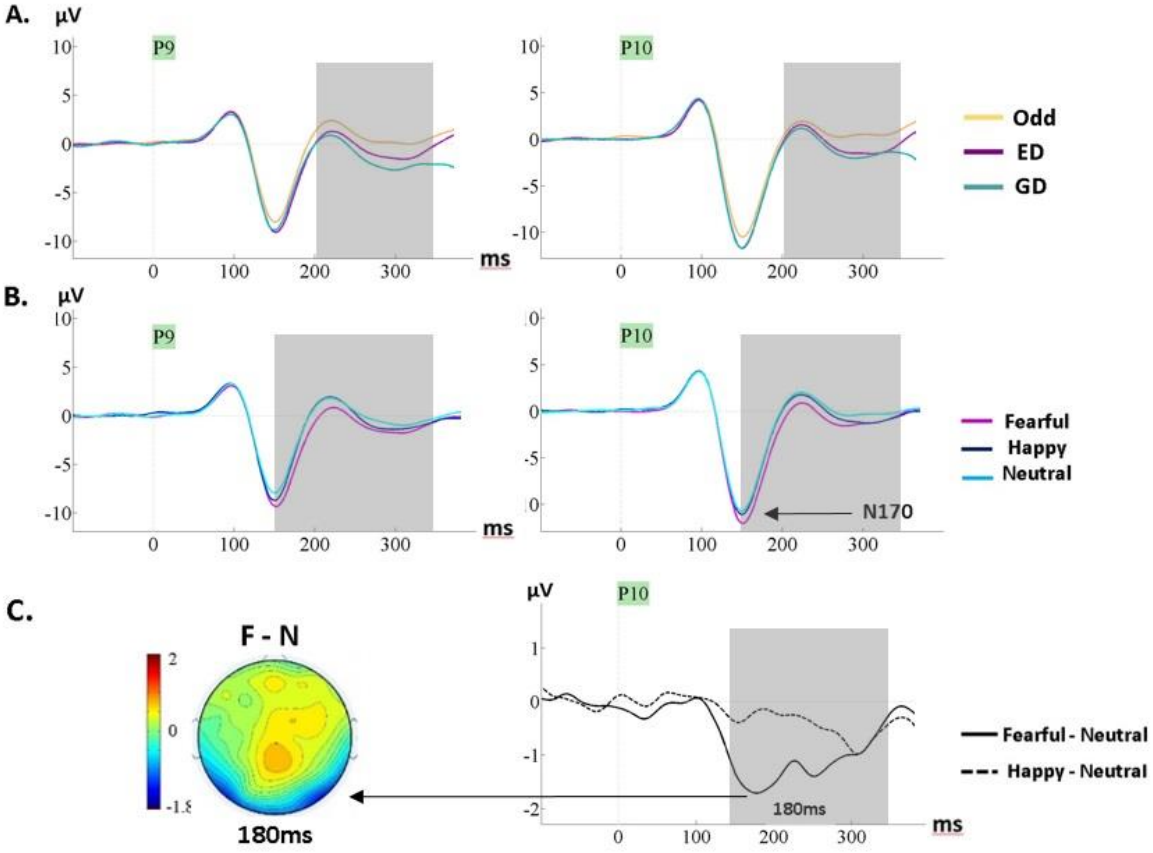


Figure 19. Effect of Task and Emotion at Lateral-Posterior Sites (Exp.4)

Grand-averages featuring the N170 component at P9 and P10 as a function of (A) task (across emotions), and (B) emotion (across tasks). (C) Grand-average difference waveforms generated by subtracting ERPs to neutral from ERPs to fearful faces (F-N, solid line) and ERPs to neutral from ERPs to happy faces (H-N, dashed line) at P10. The gray interval (150-350ms) is where the emotion effects for fear were seen. The map shows the voltage difference between fearful and neutral faces (F-N) across the scalp at the latency at which the effect was largest (180ms).

Table 18. *Exp. 4 (task comparison) statistical effects on mean amplitudes analyzed over six 50ms time windows at occipital sites (O1, Oz, O2), with F, p and η_p^2 values. LH, left hemisphere; RH, right hemisphere; ODD, oddball detection task; ED, emotion discrimination task; GD gender discrimination task; F, fear; H, happy; N, neutral. Main effects p values: p* < .05; p** < .01; p*** < .001; p**** < .0001; ns, not significant. Bonferroni-corrected paired comparison tests are also reported (e.g., F < H + N means that the main effect of emotion is due to a significantly smaller mean amplitude for fearful compared to both happy and neutral expressions).*

Main effects and interactions	50-100ms	100- 150ms	150- 200ms	200-250ms	250-300ms	300-350ms
Electrode	-	*F* = 13.37, *p*****, η_p^2 = .32 O1 + O2 > Oz	*F* = 5.34, = .019, η_p^2 = .16 O1 > Oz	*F* = 9.91, *p*** , η_p^2 = .26 O1 + O2> Oz	*F* = 10.01, *p*, η_p^2 = .26 O1 + O2 > Oz	-
Task	-	-	-	-	-	*F* = 11.76, *p****, η_p^2 = .30 ODD + ED < GD
Emotion	-	-	*F* = 6.41, *p*, η_p^2 = .19 F < H + N	*F* = 3.74, *p**, η_p^2 = .12 F < N	*F* = 5.16, *p*=.014, η_p^2 = .16 F < N	*F* = 7.62, *p*, η_p^2 = .21 F + H < N
Electrode X Task	-	-	-	-	-	*F* = 4.4, *p*=.*, η_p^2 = .14 • O1: *F* = 7.31, *p*, η_p^2 = .21 ODD < GD • O2: *F* =5.15, *p*, η_p^2 = .16 ODD < GD • Oz: *F* = 18.12, *p*****, η_p^2 = .39 ODD + ED < GD

Table 19. *Exp. 4 (task comparison) statistical effects on mean amplitudes analyzed over six 50ms time windows at lateral-posterior sites (CB1/2, P7/8, PO7/8, P9/10), with F, p and η_p^2 values. LH, left hemisphere; RH, right hemisphere; ODD, oddball detection task; ED, emotion discrimination task; GD gender discrimination task; F, fear; H, happy; N, neutral. Main effects p values: p* < .05; p** < .01; p*** < .001; p**** < .0001; ns, not significant. Bonferroni-corrected paired comparisons are also reported (e.g., F < H + N means that the main effect of emotion is due to a significantly smaller mean amplitude for fearful compared to both happy and neutral expressions).*

Main effects and interactions	50-100ms	100- 150ms	150- 200ms	200-250ms	250-300ms	300-350ms
Electrode	F = 26.02, p****, η_p^2 = .48 P9/10+P7/8 < CB1/2 < PO7/8	F = 58.88, p****, η_p^2 = .68 P9/10 < CB1/2 < P7/8 < PO7/8	F =73.14, p****, η_p^2 = .72 P9/10 < CB1/2 + P7/8 < PO7/8	F = 92.39, p****, η_p^2 = .77 P9/10 < CB1/2 + P7/8 < PO7/8	F = 79.12, p****, η_p^2 = .74 P9/10 < CB1/2 < P7/8 < PO7/8	F = 64.97, p****, η_p^2 = .70 P9/10 < CB1/2 < P7/8 < PO7/8
Hemisphere	-	-	F =7.88, p**, η_p^2 = .22 RH < LH	-	-	-
Task	-	-	-	F = 5.57, p=.01, η_p^2 = .17 GD < ODD	F = 10.51, p***, η_p^2 = .27 GD < ODD + ED	F = 4.59, p = .015, η_p^2 =.14 GD < ODD
Emotion	-	-	F =22.55 p****, η_p^2 = .45 F < H + N	F = 10.96, p***, η_p^2 = .28 F < H + N	F = 7.05, p**, η_p^2 = .20 F < N	F = 3.74, p = .03, η_p^2 = .12 F < N
Electrode X Task	-	-	-	-	F = 2.91, p = .028, η_p^2 = .09 • CB: F = 11.04, p ***, η_p^2 = .28 GD < ODD + ED • P9/10: F = 9.48 p ***, η_p^2 = .25 GD + ED < ODD • P7/8: F =9.41, p **, η_p^2 = .25 GD < ODD + ED • P07/8: ns	-
Electrode X Emotion	-	-	F =3.60 p**, η_p^2 = .11 • CB: F =19.54 p****, η_p^2 = .41; F < H + N • P9/10: F =16.39 p****, η_p^2 = .37; F < H + N • P7/8: F 14.19 p****, η_p^2 = .34; F < H + N • PO8/8: F =15.49 p****, η_p^2 = .36; F < H + N	-	-	-

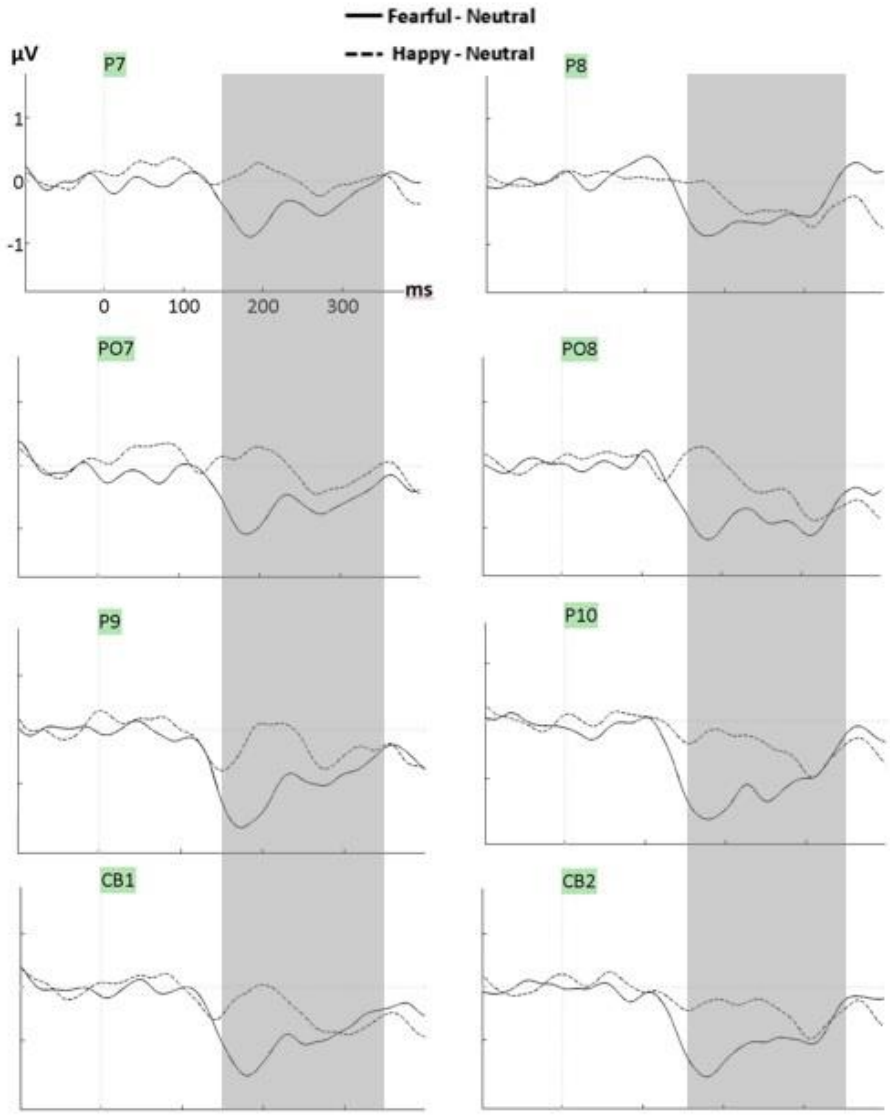


Figure 20. Fearful–Neutral and Happy–Neutral Difference Waveforms (Exp.4)

Grand-average difference waveforms generated by subtracting neutral from fearful and happy conditions (F-N and H-N) at lateral-posterior sites (CB1/2, P7/8, PO7/8, P9/10). The gray zone highlights the time windows during which the effect for fear was significant at all lateral-posterior sites (150-350ms).

5.3.2.2 Effects of Task and emotion at lateral-posterior sites (CB1/2, P9/10, P7/8, PO7/8)

N170 Peak Amplitude. The N170 amplitude was larger in the right compared to the left hemisphere (main effect of hemisphere, $F(1, 28) = 9.51$, $p < .01$, $\eta_p^2 = .25$). No main effect of task was seen ($p = .69$), or task by emotion interaction ($p=.56$). However visual inspection of the grand-averages suggested an effect of task at P9/P10 sites (Figure 19A). Given the task effect on the N170 reported in a recent meta-analysis (Hijonosa et al., 2015), I decided to analyze P9/10 separately[14] and found that there was indeed a small main effect of task at these electrodes ($F(1.60, 44.76) = 3.46$, $p = .05$, $\eta_p^2 = .25$; significant paired comparison $p < .05$) such that N170 amplitudes were smaller for the ODD compared to the ED task ($p= .021$; no significant differences for ODD-GD or ED-GD comparisons).

As seen on Figure 19B, the N170 amplitude was also larger for fearful compared to both happy and neutral expressions which did not differ (main effect of emotion, $F(1.93, 54.11) = 9.51$, $p < .001$, $\eta_p^2 = .25$; significant comparisons for fear-neutral at $p = .001$ and fear-happy at $p = .02$). No interaction between task and emotion was seen.

Mean Amplitude analyses over Six Time Windows (CB1/2, P7/8, P9/10, PO7/8).

Statistical results for these analyses (50-350ms) are reported in Table 19 and visually depicted in Figures 18, 19, and 20.

An effect of task was seen between 200 and 350ms with more negative amplitudes (smaller) for the GD task compared to the ODD task, with amplitudes for the ED task in between

[14] Note that for this analysis, N170 was re-measured at P9/10 for all subjects; however, N170 was maximum at these sites for 16/29 participants for P9 and for 20/29 participants for P10, see Table 14

(Fig 19A). Between 250-300ms, amplitudes were also significantly more negative for the GD than the ED task at CB1/2 and P07/8 sites (emotion by electrode interaction).

An effect of emotion was first seen between 150 and 200ms, with smaller amplitude for fearful faces compared to neutral and happy faces (Fig. 19B-C). The fear effect (fearful versus neutral faces) peaked around 180ms but was seen until 350ms (Fig. 18, 19B-C, Fig.20). Between 150 and 250ms, amplitudes were also more negative for fearful than happy faces. However, amplitudes for happy faces were never significantly smaller than those for neutral faces in any time window. There were no interactions between emotion and task in any time window.

5.5 Discussion

Various experimental tasks have been used during the ERP recording of emotional faces and reports of early emotion effects have been inconsistent. While task was varied in Exp.'s 1 to 3 (with different participants completing the different tasks) a more powerful means of measuring the impact of task is to test task within-subjects. The present study directly tested the impact of task demands on the neural processing of fearful and happy expressions.

The experiments presented in this thesis are of the first few to focus on effects of happy expressions at occipital sites. In Exp.'s 1 to 3, a happy effect was seen beginning ~100ms and peaking at ~120ms at medial occipital site Oz. This happy effect spread more laterally around 150ms and was sustained until 350ms. In the current task comparison study, only a very weak and temporally localized happy effect was seen on medial site Oz between 110 and 120ms (not significant on P1) and between 300 and 350ms at medial and lateral occipital sites. There was also no effect seen for happy faces at lateral-posterior sites. A critical difference between the

current study (Exp.4) and Exp.'s 1 to 3 was the manipulation of fixation location. In the current study, participants were always fixated on the center of the face (tip of the nose) whereas fixation also fell on the eyes and mouth in Exp.'s 1 to 3. In those studies, emotion interacted with fixation location at occipital sites between 150 and 200ms such that the fear and happy effects were seen only when participants were fixated on the mouth. This interaction was seen earlier at occipital sites for happy expressions only, between 100 and 150ms in Exp.3 and in all tasks at lateral-posterior sites seen during P1-N170 amplitude difference. The fact that the early happy effect was only weakly seen around 115ms in the current study, when fixation did not fall on the mouth, supports the interpretation (initially proposed by Halgren et al., 2000) that this early happy effect reflects the fast discrimination of diagnostic cues such as the smile, based on local luminance and contrast, within 100-120ms in early visual areas (V1/V2), which is then relayed rapidly to the amygdala by direct V2-amygdala connections. The fact that previous studies have used a central fixation (landing on the tip of the nose or nasion) may explain why this early happy effect was not often reported.

Early effects for fearful faces have been debated. Most studies have reported no modulation of the P1 by emotion (Palermo and Rhodes, 2007; Vuilleumier and Pourtois, 2007); however, a few using emotion-irrelevant tasks have reported enhanced P1 for fearful compared to neutral faces in gender discrimination tasks (Pourtois et al., 2005; Wijers et al., 2012), oddball detection tasks (Batty and Taylor, 2003; Williams et al. 2004), and passive viewing of emotional faces (Blau et al., 2007; Smith et al., 2013). Studies reporting this early effect have suggested rapid and automatic (i.e., involuntary) processing of intrinsically threatening fearful faces via a subcortical route involving the amygdala. In Exp. 1 (GD task) no effect of fear was seen on the P1

itself; however, an early effect of fearful expressions was localized to the left hemisphere during the 50-100ms time window, peaking around 80ms. This early effect for fearful faces was not replicated in the current study. Given its early timing and its extremely localized occurrence, this effect is most likely not a true task effect but rather a result of group differences. In the current study comparing emotion-relevant and emotion-irrelevant tasks there was also no modulation of the P1 by fearful expressions seen when mean stimulus contrast and pixel intensity were controlled for. This was also true for Exp.'s 1 to 3 when these same tasks were tested separately. Together, the findings of the present thesis suggest that previous reports of P1 modulations by fearful faces may have been driven by the stimuli differences in low-level characteristics such as contrast or luminance which were not controlled for (e.g., Batty & Taylor, 2003; Pizzagalli et al., 2002).

In the present experiment, modulations of ERPs by fearful faces were seen starting at the N170 component (~150ms) and all the way until 350ms at lateral-posterior sites (and to a lesser extent at occipital sites), regardless of task demands. This enhanced negativity for fearful faces seen also in Exp.'s 1 to 3, likely reflects activity linked to the processing of fear added onto the normal activity related to processing neutral faces, as proposed by other groups (Rellecke et al., 2013; Schacht and Sommer, 2009). This added negativity started at the N170 but was seen mostly after the peak (during the timing of the visual P2 and EPN, Rellecke, Sommer, & Schacht, 2013; Rellecke et al., 2011; Schupp et al., 2004), suggesting it was different from the structural encoding reflected by the N170 component.

The main goal of the current study was to test the impact of task demands on the neural processing of fearful and happy expressions. Importantly, there was no interaction between

emotion and task between 50 and 350ms post-stimulus (including P1, N170 and EPN), at occipital or posterior lateral sites. The inconsistencies reported in the literature for P1 and N170 are thus unlikely due to differences in task demands. Instead, the current data are in line with previous groups reporting enhanced negativity at lateral-posterior sites for fearful expressions (and to a lesser extent for happy expressions) beginning ~150-200ms post-stimulus (encompassing the visual P2 and EPN) and this negativity is sometimes captured by the N170 component. The exact reason why the effect is sometimes seen on the N170 remains unclear; however, the current study demonstrates it is not due to differences in attention to the face placed by task demands.

While task did not interact with emotion, there was a main effect of task. This effect was seen beginning at the N170; however, this effect was not clearly established until ~200ms and lasted until 350ms. Overall, a reduced negativity was seen for the ODD task (more positive amplitude) compared to the GD task, with ED task in between. It is possible that this effect of task is a result of differences in task difficulty or differences in the amount and/or level of processing (e.g., Craik & Lockheart, 1972) between the tasks. The main effect of task on the neural processing of facial expressions was not a specific aim of this study and importantly it did not interact with facial expression. Future studies however may want to explore the impact of task demands on face processing.

To summarize, the current study investigated the impact of task demands on the neural processing of fearful and happy expressions. An effect of task started at the N170 and was clearly established after 200ms (i.e., EPN). Replicating Exp. 1 to 3, an enhanced negativity at lateral-posterior sites was seen for fearful expressions from ~150-300ms post-stimulus; however, the happy effect at occipital sites occurred weakly. Importantly, the emotion effects occurred

independently of task. The current results suggest that emotion effects for fearful and happy expressions occur irrespective of task-relevance and previous inconsistencies in the facial expression ERP literature are unlikely due to task demands.

Chapter 6: General Discussion

Previous results from research investigating the time course of facial expression processing have been inconsistent. The main aim of this thesis was to investigate the impact of fixation to facial features on the neural processing of facial expressions (Exp.'s 1 to 3). Using eye-tracking to enforce correct fixation to facial features, I tested the effect of fixation to facial features on scalp-recorded ERPs measured between 50 and 350ms, encompassing well studied face and emotion-sensitive components (P1, N170 and EPN) during a gender discrimination – GD (Exp.1), emotion discrimination –ED (Exp.2) and an oddball detection –ODD (Exp.3) tasks. I also aimed to test whether attention to the face placed by task demands influences facial expression processing by directly comparing the GD, ED and ODD tasks completed by the same participants in Exp.4. Within this final chapter, results from all of the studies will be summarized to address both of these aims and will be discussed in terms of their implications for our understanding of early face and facial emotion perception.

6.1 Impact of fixation to facial features during facial expression processing

6.1.1 Importance of gaze-contingent procedure in ERP face research

An important contribution of this thesis is that it is the first known series of studies to investigate the impact of fixation to facial features of facial emotions using a gaze-contingent procedure. The studies presented in this thesis combined eye-tracking and EEG in order to achieve controlled fixation on facial features (left eye, right eye, nose and mouth in Exp.'s 1 to 3 and the nose in Exp.4). Testing fixation to facial features within the context of the whole face is a novel paradigm and has never been published, to the best of my knowledge, in ERP emotion research. All trials in which participants made an eye movement away from the desired fixation

location were eliminated. This resulted in a very high attrition rate and a loss of 43 tested participants, many more than typical in classic EEG experiments. The fact that a high number of trials were removed indicates that many participants made quite a lot of eye movements even with a brief (i.e., 257ms) presentation time. Given the size of the stimuli, these eye movements were sufficient in size to allow fixation on facial features other than the to-be-fixated feature. In previous studies that did not enforce fixation to the face (i.e., the entire literature on ERPs and emotion) participants most likely made shifts in gaze. As such, researchers conducting these studies could never be sure exactly where participants were looking. Therefore despite the high attrition rate associated with this paradigm the results presented throughout this thesis highlights the need for controlling for fixation to the face during face and facial emotion ERP research.

6.1.2 Different sensitivity of P1 and N170 to fixation location during face perception

Effects of fixation to features using a gaze-contingent procedure has only been tested on the N170 (de Lissa et al., 2014; Nemrodov et al., 2014) for expressionless faces. Therefore in the current thesis I tested whether fixation impacted well-known face and emotion-sensitive components P1, N170 and EPN.

In the current gaze-contingent paradigm faces were moved around a central fixation location in order to achieve fixation on desired facial features. This manipulation resulted in differential amounts of facial information presented in the visual fields, with fixation location effects on the P1 component. The P1 component is an early visual response generated within the extrastriate cortex that occurs ~80-120ms post-stimulus onset at occipital sites. The P1 is well-known to respond to the low-level characteristics of stimuli including contrast, luminance, color

and spatial frequencies (Rossion and Jacques, 2008) and is also sensitive to attentional effects (Luck, Woodman, & Vogal, 2000; Mangun, 1995). In the current thesis, the clear hemifield effect on the P1 amplitude (seen also on P1-N170 peak difference) that I discussed in Section 2.4.2 (i.e., larger P1 amplitude for the right than for the left eye on the right hemisphere and vice versa for the left hemisphere) was virtually identical across Exp.'s 1 to 3. This hemifield effect was also reported in the first studies using the gaze-contingent procedure with expressionless faces (de Lissa et al., 2014; Nemrodov et al., 2014; Zerouali et al., 2013). In addition, the P1 sensitivity to face position was also revealed by a delayed and larger P1 response seen when fixation was on the mouth compared to each of the other locations (although less clearly for Exp. 3 – ODD task). It is possible that this result is due to the fact that the visual system is more sensitive to facial information in the upper visual field given faces are most often seen in that area. More facial information is indeed present in the upper visual field when fixation is on the mouth compared to the eyes and nose.

The N170 was found to be sensitive to fixation location with a larger amplitude for fixation to the left and right eyes compared to the nose and the mouth. When controlling for low-level stimulus differences, the N170 reliably differs between object categories while the P1 does not, supporting the commonly held belief that both components reflect distinct stages of visual processing with only the N170 reflecting high level vision and face categorization (e.g., Ganis et al., 2012; Jemel et al., 2003; Rossion & Caharel, 2011; Tarkiainen, Cornelissen, & Salmelin, 2002; and see Desjardins & Segalowitz, 2013). This, along with the reasons I have outlined in Section 2.4.2, proves that this fixation effect is not attributable to face position but rather reflects a true eye sensitivity. This effect was remarkably similar across emotions and across Exp.'s 1 to 3

demonstrating that this eye sensitivity occurs to the same extent for faces expressing fear and happiness and is thus largely facial-expression-invariant and task-invariant. While the effect of fixation to the eyes was not directly tested between tasks, the series of studies speaks to task-invariance such that the eye sensitivity was seen in three separate tasks varying in degrees of attention required to the face. The eye sensitivity within full faces as shown here in three separate experiments, provides further support for Nemrodov et al.'s (2014) hypothesis of an eye-detector during the processing of the structure of the face. It is to be noted that mean pixel intensity (PI) and contrast did not differ between pictures; however, local PI and contrast did. In particular higher contrast and lower PI were seen for the eyes compared to the nose and mouth. Therefore the hypothesized eye detector might rely on low-level cues such as local contrast and pixel intensity, a possibility that will have to be tested by future studies.

In contrast to the P1 and N170 components, there was no effect of fixation location after ~200-250ms at lateral-posterior sites (where visual P2 and Early Posterior Negativity -EPN were seen) and this was true across Exp. 1 to 3. This result is in line with the idea that the eye sensitivity is specific to the face structural encoding stage as indexed by the N170. Together these results illustrate nicely the temporal dynamics of the neural systems involved in face perception as outlined in classic face perception models (e.g., Bruce & Young, 1986; Haxby, Hoffman, & Gobbini, 2000). Low-level facial information is first detected in the visual system by the early visual areas as reflected by P1 sensitivity to face position. Processing of the structure of the face occurs later, as reflected by the N170 suggested to be generated by face-sensitive areas including the fusiform gyrus (FG), superior temporal sulcus (STS) and inferior occipital gyrus (IOG); during

that stage, a special sensitivity to eyes is seen. No sensitivity to fixation was seen after the N170 during the stages in which semantic information (e.g., expression of emotion) are encoded.

6.2 Emotion processing occurs independently of face processing

Classic models of face perception suggest that face identity and facial expressions are processed independently (Bruce & Young, 1986; Haxby et al., 2000); however, reviews of EEG and fMRI studies have argued against the idea that these two processes are completely separate (Calder & Young, 2005; Vullieumier & Pourtois, 2007). In the current thesis I used ERPs as a tool to examine whether structural and emotional aspects of face encoding are independent or interacting processes. The N170, peaking around 170ms at occipital-temporal sites, is a well-known marker of face processing and is thought to reflect the structural encoding of the face (e.g., Bentin, Allison, Puce, Perez, & McCarthy, 1996; Ganis, Smith, & Schendan, 2012; Jemel et al., 2003; Rossion et al., 2000; Rossion & Caharel, 2011). The effect of facial emotions on the N170 has been debated with several studies reporting no modulation by emotion (see review by Eimer & Holmes, 2007; and see Rellecke et al., 2013) while others did report increased N170 with fearful compared to neutral expressions (e.g., Batty and Taylor, 2003; Blau et al., 2007; Jetha et al., 2012; Leppänen et al., 2008). The current studies addressed this debate by testing whether or not processing of a facial feature (which is integrated into the face percept during structural encoding at the level of the N170) interacted with processing of facial expressions on the N170. Emotion effects seen for fearful and happy expressions did not interact with fixation location on the N170, and this was true in all Exp.'s 1 to 3. This suggests that the eye sensitivity (discussed above in Section 6.1.2) is largely independent of facial expression of emotion in both emotion-

relevant and emotion-irrelevant tasks and thus argues for separate processing of face structure and facial emotion.

6.3 Different spatio-temporal distributions for fearful and happy expressions

6.3.1 Lack of support for P1 sensitivity to fearful faces

Neuroimaging and clinical neuropsychological research has implicated the amygdala in the extraction of emotional content from facial expressions (see Vuilleumier & Pourtois, 2007 for a review). In particular, amygdala activation has been most commonly associated with the detection of fearful expressions (Adolphs et al., 2005; Morris et al., 1996; Phillips et al., 1998; Whalen et al., 2004). Neuroimaging research suggests that fearful faces activate a subcortical route (including the amygdala) that bypasses the cortical route, allowing for the rapid detection of fearful threatening faces (*Threat hypothesis*, LeDoux, 1996; Morris et al., 1998). For this reason, the study of fearful faces has dominated the ERP literature, testing for an early effect for fearful faces. While a few studies have reported an enhanced P1 for fearful compared to neutral faces (Batty and Taylor, 2003; Pourtois et al., 2005; Smith et al., 2013; Wijers et al., 2012), other studies report no modulation of the P1 by emotion (Palermo and Rhodes, 2007; Vuilleumier and Pourtois, 2007). Importantly, in some of these previous studies, stimuli low-level differences were often not controlled for (e.g., Batty & Taylor, 2003).

Using stimuli that did not significantly differ in overall mean pixel intensity and contrast, Exp.'s 1 to 4 revealed no modulation of the P1 by fearful faces over neutral. In the GD task there was a modulation by fearful expression *before* the P1 at ~80ms for fearful faces that was localized to PO7 and P7 electrodes (Fig.4-6). This very early fear effect was, however, not replicated during

a direct comparison of tasks in Exp. 4 suggesting the effect was specific to the group. One possibility is that individual differences were driving this very early effect. There is suggestion that trait anxiety influences the processing of threat-related information (including fearful faces, Bar-Haim et al., 2007) and anxiety level has been shown to modulate early stages of information processing as reflected by the P1 (Walentowska & Wronka, 2012; Morel et al., 2014). Numerous neuroimaging studies have indeed shown increased amygdala activity in high trait anxious individuals during unconscious processing of fearful stimuli (Bishop, 2007; Etkin et al., 2004) when compared with low anxious individuals. Shyness trait has also been related to early processing of fearful faces (Jetha, Zheng, Schmidt, & Segalowitz, 2012). Jetha et al. (2012) reported an increased P1 amplitude for fearful compared to neutral faces in low-shy compared to high-shy individuals. It is to be noted that in the current thesis the P1 was not modulated by fearful expressions; however, there was a very early effect in Exp.1 *before* the P1 that may have been modulated by these individual differences. Whether or not individual differences are associated with early fear effects on the P1 provides a future direction for this ERP emotion research.

The current series of experiments found no modulation of the P1 by fearful expressions and this was true in both emotion-relevant and emotion-irrelevant tasks. Therefore, the current thesis does not provide support for greater activation of early visual brain areas to intrinsically salient, threat-related stimuli (threat gist) as proposed by Luo et al. (2010) and reviewed in Vuilleumier and Pourtois (2007). Instead, the current results support findings of an effect for fearful expressions starting around or right after the N170 (Eimer et al., 2003; Eimer & Kiss, 2007; Leppänen et al., 2007; Leppänen et al., 2008; Schupp et al., 2004), as discussed next.

6.3.2 Effects of fearful expressions seen mostly at lateral-posterior sites

Modulations of ERPs by fearful faces were seen right around the latency of the N170 (~150ms), peaking around 180-200ms, lasting until ~300ms and this was true for Exp.'s 1 to 4. This fearful effect was mostly seen at lateral-posterior sites (and to a lesser extent at occipital sites) and encompassed the visual P2 (~200ms) component and the EPN – a well-known marker of emotion processing (Rellecke et al., 2013; Rellecke et al., 2011; Schupp et al., 2004). The effects for fearful expressions reported in this series of studies are in line with previous reports of emotion effects starting around or right after the N170 and lasting 100ms or more (Eimer et al., 2003; Eimer and Kiss, 2007; Leppänen et al., 2007; Schupp et al., 2004; Sprengelmeyer and Jentzsch, 2006) as previously discussed in Section 2.4.3. This "added emotional effect" for fearful expressions likely reflects activity linked to the processing of fear added onto the normal activity related to processing of the structure of the face in cortical visual areas, as proposed by other groups (Schacht and Sommer, 2009; Schupp et al., 2004; Rellecke et al., 2013). The timing of this fear-related process coincides with amygdala activation reported in intracranial ERP studies in response to fearful faces ~150-200ms post-stimulus (Meletti et al., 2012; Krolak & Salmon, 2004; Pourtois, Spinelli, Seeck, & Vuilleumier, 2010a) as well as in a recent MEG study (Dumas et al., 2013). However amygdala activity *per se* is very unlikely recorded on the scalp with EEG and this fear effect is thus more likely the result of the enhancement of the activity of perceptual visual areas, such as the face-sensitive fusiform gyrus, by the amygdala. Modulations of the fusiform

gyrus by the amygdala has indeed been reported by a few intracranial studies (Pourtois, Spinelli, Seeck, & Vuilleumier, 2010b) and MEG studies (e.g., Dumas et al., 2013) in a similar time window.

6.3.3 Effect for fearful expressions: It's not just about the eyes

The wide open eyes are particularly salient for fearful expressions and are used most prominently when discriminating fear from other expressions (e.g., Calder et al., 2000). Recent ERP research that forced feature-based processing have suggested the importance of the eye region in the neural response to fearful expressions at the level of the N170 or later (Leppänen et al., 2008; Schyns et al., 2007, 2009). When presenting whole facial expressions, as seen in everyday life, results from the current thesis demonstrate that both the eyes and mouth are important for processing fearful expressions. In Exp.'s 1 to 3, an effect for fear was seen between 150 and 200ms at occipital sites during fixation to the mouth only. In Exp.2 (ED) and Exp.3 (ODD), this interaction was also seen at lateral-posterior sites between 250-350ms (i.e., timing coinciding with EPN). The effect for fearful expressions was also seen during fixation to the eyes (no effect during nose fixation) between 250 and 350ms in Exp.2 and between 200 and 250ms in Exp.3. Thus, fearful cues in the eyes and mouth seem to both impact neural activity during the semantic processing of the emotional content of the face. This is in line with the results of Leppänen et al. (2008) where the added negativity in response to fearful expressions (between 160 and 240ms) was eliminated when the eye region was covered. One novel contribution of this thesis is the finding that the fearful mouth is also important during processing of fearful expressions, which was not tested in the Leppänen et al., study. This result supports recent behavioural studies that have demonstrated the importance of the mouth region in the recognition of fearful expressions.

During free viewing of the entire face participants made ocular eye movements equally towards the eyes and mouth of fearful faces (Eisenbarth & Alpers, 2011). Also, a recent study using *Bubbles* reported that the mouth area, even more than the eyes, is used to discriminate between the basic emotions (fear, sadness, happiness, anger and disgust) and neutral. Participants did use information from the eye region, though less so than the mouth region (Blais et al., 2012).

It is important to note that the effect for fearful expressions was seen regardless of fixation location in Exp. 1 (GD). The reasons for the lack of an interaction between expression and fixation location during this gender categorization task is unclear. The failure to find this interaction might be related to this particular task (GD) in this particular design (face moving around the screen from one trial to the next). The effect for fearful expressions was also seen in Exp. 4 regardless of task when fixation was restricted to the nose – a finding that replicates other studies using a central fixation (landing on the nasion or tip of the nose) (e.g., Rellecke et al., 2011; Rellecke et al., 2013; Schupp et al., 2004). In previous studies, fixation was not enforced, however, allowing for the possibility of shifts in gaze to the eyes and/or mouth, possibly driving the reported fear effects. Fixation was enforced in the current Exp.4 however, and the effect was still seen. One could argue that because the face always appeared in the exact same position on the screen in Exp.4 it is possible that participants maintained fixation on the nose, but moved their attention covertly to the different facial features (perhaps pre-attending these locations even before the face was presented). In order to address these inconsistencies, future studies should test a direct comparison of task while manipulating fixation to facial features (other than nose) in order to better probe the possible influence of task demands on the use of various facial features during the processing of facial expressions.

6.3.4 An early and later effect for happy expressions seen mostly at occipital sites

Fearful and angry expressions involve signals of a potential threat whereas happy expressions convey signals of a potential benefit (Darwin, 1872). From a biological point of view, it is more advantageous to avoid a potential threat than to attend to a potential benefit in the environment. Following this adaptive view, we would expect our neurocognitive system to prioritize the recognition of threat-related compared to non-threat related facial expressions (Williams et al., 2006). Yet, this seems to be at odds with categorization tasks where facial expressions are explicitly identified. A consistent happy-face advantage has been shown using behavioural measures (e.g., Calder, Young, Keane, & Dean, 2000; Calvo & Lundqvist, 2008, Palermo & Coltheart, 2004; Tottenham et al., 2009) such that happy expressions are recognized more accurately and faster in studies comparing all basic emotions including neutral faces (Calder et al., 2000; Palermo & Colheart, 2004), when comparing subsets of emotions (e.g., Leppänen & Hietanen, 2004; Juth, Lundqvist, Karlsson, & Ohman, 2005) and with various stimulus sets (Palermo & Coltheart, 2004). Despite this robust finding of superior and more rapid recognition of happy expressions, the study of threatening (i.e., fearful and angry) expressions has dominated the ERP literature. Although inconsistencies exist between studies, reports of early emotion effects as reflected by the P1 and N170 components have generally reported a negativity bias with increased responses mostly for negatively valenced (fearful or angry) expressions. A negativity bias has also been demonstrated for the EPN (e.g., Sato et al., 2001; Schupp et al., 2005); however, the EPN has also been shown to reflect a general emotional response including both happy and fearful expressions (e.g., Rellecke et al., 2011; Schacht & Sommer, 2009; Schupp et al., 2006).

In classic ERP studies with emotion, early effects are commonly measured at P1 and N170 peaks. Systematic analysis of the current data, however, revealed emotion effects at timings between the classically studied peaks. Importantly, this revealed an early happy effect, seen across emotion-relevant and emotion-irrelevant tasks in Exp.'s 1 to 3. These results present a very localized happy effect at a midline site for P1 rather than at the classically measured sites (O1/O2). Such midline effects may have been missed by previous studies. This happy effect started on the P1; however, it was maximal *after* the P1 (115-120ms). No such effect was seen for fearful faces, suggesting this happy effect is specific to the processing of happy faces and unlikely a general emotion effect or a simple attentional effect. These results suggest more rapid processing of happy than fearful expressions, which is in line with behavioural reports of faster discrimination of happy faces compared to the other basic emotions. This rapid processing of happy expressions is likely due to rapid discrimination of smiling mouth cues – a finding I will expand upon below.

6.3.5 Importance of the mouth during happy expression processing

The early effect for happy faces seen in Exp.'s 1 to 3 may have been driven by information provided by the mouth. This consistent effect was seen in this series of studies which forced fixation on key facial features. Recall that interaction of this early happy effect with fixation location was seen in Exp.1 to 3. At occipital sites between 150 and 200ms the happy effect was seen *only* for fixation on the mouth. A similar interaction was also seen earlier in the P1-N170 analysis at lateral sites. In Exp. 4, when fixation always landed on the center of the face (tip of the nose), no early happy effect was seen significantly. Visual inspection of the 2D voltage map of the happy-neutral difference revealed there may have been such a mouth effect (this was

confirmed by mean amplitude analysis between 110 and 120ms) but this effect was very weak. This effect was only seen again much later between 300 and 350ms at occipital and lateral-posterior sites. Together, these results from Exp.1 to 4, suggest that the early processing of happy expressions is driven by information from the mouth region.

A similar proposal was made by Halgren and colleagues. Halgren et al. (2000) recorded magnetic fields in response to various stimuli including happy and sad faces while participants identified repeated faces. Results indicated a midline occipital source (around areas V1-V2) that discriminated happy from neutral expressions between 100-120ms post-stimulus. That source was separate from the more lateral and later source that corresponded to the magnetic equivalent of the N170, and was also sensitive to more sensory aspects of the stimuli. They proposed that a fast discrimination of diagnostic cues such as the smile, based on low-level properties such as luminance and contrast, could occur within 100 and 120ms in those early visual areas and then be relayed rapidly to the amygdala by direct V2-amygdala connections. This provides a possible explanation for the happy effect reported in the current thesis given the local pixel and contrast differences between emotions seen for the mouth area of our stimuli. The current findings however, further suggest that the importance of information provided by the mouth region during the processing of happy expressions was also seen all the way until at least 350ms. From 150 to 350ms, the happy effect was also seen at lateral-posterior electrode sites and the happy effect was only seen during fixation to the mouth between 200 and 350ms in Exp.2 (ED) and 3 (ODD). This suggests that the mouth also provides a cue for the semantic processing of the emotional content of the face that occurs during the added negativity for happy expressions (coinciding with the timing of the EPN).

Similar to the fearful effect, interactions with fixation location during the semantic processing of emotional information (i.e., 200-350ms post-stimulus) were not seen in Exp. 1 (GD task). As discussed above, a direct comparison of task while manipulating fixation to facial features of facial expressions would be required to better understand this result.

6.3.6 Task did not interact with fearful and happy effects (at occipital and lateral-posterior sites)

Previous ERP research investigating facial expression processing has used various experimental procedures. Only two known studies in the literature directly compared task in a within-subjects design, both of which tested angry and not fearful expressions. Small differences also existed in the distribution of the effects seen in the current Exp. 1 -3 that varied in task, suggesting possible task related effects. For a more powerful test of task, I directly tested the impact of task (within-subjects design using tasks used in Exp.'s 1 to 3) on the neural response to fearful and happy expressions in Exp. 4. In order to avoid fatigue effects, fixation location was not manipulated. For all tasks fixation was restricted to the tip of the nose, as typically done in face ERP research. The results revealed no interaction between task and the effects of emotion for fearful and happy expressions (as discussed above). Therefore inconsistencies seen in the literature for early emotion effects and small differences between the current studies in Exp.'s 1 to 3 are not likely a result of differences in task demands.

While task demands did not interact with fearful and happy emotion effects, main effects of task were seen. Smaller amplitudes for the ODD task compared to the GD and ED tasks was seen clearly between ~200-350ms. This effect of task likely reflects differences in the level of

processing of the face required by the tasks. A deeper processing may be required for gender and emotion judgments compared to a judgment of a face vs. non-face.

It is important to acknowledge that lack of emotion and task interaction may be limited to the scalp distribution (i.e., occipital and lateral-posterior) measured/analyzed and the tasks used in the current study. I measured/analyzed only a subset of scalp electrodes. There may potentially be interactions between task and emotion, elsewhere (e.g., frontal distribution). The current study, however, analyzed posterior distributions where visual processing occurs. Still, an opportunity for future studies is to measure emotion effects, and the interaction with task, at other scalp locations.

Finally, it is to be noted that the order of the presentation of tasks may have influenced the results. For example, completing the ED task first could have primed participants to attend to the emotional faces in the following ODD task differently. Task order was completely counterbalanced between participants; however, the total number of participants in each condition (~5 per condition) was too small for a meaningful analysis to be reported here. An investigation of task order, requiring many more participants, is another opportunity for future studies.

6.4 Conclusions

The series of studies presented in this dissertation are the first to test the impact of fixation to facial features and to directly test the impact of task demands on the processing of fearful and happy expressions using whole faces. Combining EEG and eye-tracking using a gaze-contingent procedure novel to ERP face research, differential effects of fixation and emotion were revealed at various ERP components during gender discrimination (Exp.1), emotion

discrimination (Exp.2) and oddball detection (Exp.3) tasks. Differential effects for fearful and happy expressions were seen at posterior sites, earlier and mostly occipital for happy expressions and mostly lateral for fearful expressions. These emotion effects were also seen when these tasks were compared within-subjects in Exp. 4. Importantly no given task seemed to potentiate these emotional effects. Happy cues from the mouth are required for early processing of happy expressions (i.e., happy gist), likely driven by low-level differences, and for the later semantic processing of the emotional content of the face. Fearful cues from both the mouth and the eyes are important for semantic processing of the emotional content of the face. Importantly, no interaction between emotion and fixation location was seen on the N170, arguing for separate processing of structural and emotional aspects of the face. Differential effects of fixation location were seen for the P1 and N170, with a sensitivity to face position (low-level) on the P1, followed by an eye sensitivity seen on the N170 component, possibly reflecting the activity of an eye-detector in the processing of the face structure. In line with the idea that the eye sensitivity is specific to the face structural encoding stage, no effects of fixation were seen after the latency of the N170, suggesting this stage is associated with processing of semantic information (i.e., emotion).

This thesis has highlighted the need for controlling for fixation in ERP emotion research. The thesis also underscores the importance of quantifying neural activity *around* P1 and N170 peaks. Emotion effects may be missed by restricting measurements strictly to the peaks of these commonly studied ERP markers. The current results also help to elucidate the much debated "early" emotion effects in the temporal domain and extend our current understanding of the role of facial features and task demands during facial expression processing.

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Appendix

A1. Final trial number in GD (Exp. 1)

	Final Trial Number											
	Fear				Happy				Neutral			
Partic.	Left Eye	Right Eye	Nose	Mouth	Left Eye	Right Eye	Nose	Mouth	Left Eye	Right Eye	Nose	Mouth
1	49	62	64	66	59	65	59	67	52	62	63	58
6	60	61	61	62	63	64	57	60	68	62	61	62
8	55	55	56	48	43	42	46	48	52	55	52	48
9	59	51	53	55	54	55	61	45	51	59	58	51
10	54	52	66	59	68	47	60	64	61	55	54	56
11	54	55	53	54	55	54	44	48	48	55	52	45
14	59	59	53	62	59	61	66	65	66	68	60	58
16	52	55	58	49	60	61	54	56	64	58	59	60
19	53	60	57	56	50	60	53	58	64	55	54	53
20	52	54	50	53	48	46	51	46	43	47	46	49
23	55	55	66	59	57	61	62	58	52	58	65	57
29	53	57	55	54	61	58	67	60	54	54	58	55
30	69	62	70	70	67	67	70	62	69	70	71	70
31	46	56	54	60	53	53	57	52	48	48	64	54
62	64	67	54	64	62	61	55	57	59	63	65	58
65	59	62	56	63	70	69	59	65	63	69	61	62
67	40	53	45	50	64	50	51	52	53	50	50	43
69	44	44	47	40	42	40	45	40	42	56	46	51
70	46	43	48	45	50	54	50	51	54	52	56	49
75	56	56	56	63	61	65	61	65	64	66	70	64

A2. Final trial number in ED (Exp. 2)

	Fearful				Happy				Neutral			
Partic. Number	**Left Eye**	**Right Eye**	**Nose**	**Mouth**	**Left Eye**	**Right Eye**	**Nose**	**Mouth**	**Left Eye**	**Right Eye**	**Nose**	**Mouth**
1	61	60	61	51	52	59	52	51	47	59	58	51
2	51	55	63	52	42	52	63	65	47	57	57	49
3	56	61	61	54	67	66	59	58	68	71	58	64
8	53	51	55	56	59	52	55	59	42	48	52	51
9	61	70	73	68	73	71	67	75	73	67	73	69
12	60	68	71	67	62	73	64	74	65	72	68	64
13	42	44	40	35	44	49	38	39	41	49	45	44
14	64	67	64	47	67	66	62	49	61	71	51	47
15	52	60	63	64	60	64	62	72	58	61	66	68
18	67	76	70	69	71	74	73	71	70	71	76	73
20	74	75	73	74	74	75	69	76	52	64	73	66
22	70	74	68	66	74	73	73	69	65	73	64	68
26	51	56	47	53	54	47	55	55	45	60	57	59
44	72	73	77	75	69	69	75	72	71	63	70	75
46	62	59	68	61	69	59	58	58	52	55	50	58
47	56	54	51	61	62	60	51	54	57	48	56	53
51	63	68	66	68	70	71	68	72	74	64	72	71
52	59	48	63	66	55	53	65	67	61	58	60	71
60	71	75	75	72	63	70	69	67	71	64	73	73
62	49	61	57	52	50	51	51	49	51	60	53	56

A3. Final trial number in ODD (Exp. 3)

	Fear				Happy				Neutral			
Partic. Number	**Left Eye**	**Right Eye**	**Nose**	**Mouth**	**Left Eye**	**Right Eye**	**Nose**	**Mouth**	**Left Eye**	**Right Eye**	**Nose**	**Mouth**
4	44	39	43	39	45	37	41	49	43	36	40	46
5	59	67	64	63	58	64	60	65	61	58	59	67
8	42	81	43	55	56	47	54	50	50	50	50	53
12	54	52	49	55	52	55	50	52	50	52	47	55
13	72	73	75	69	71	77	71	68	71	75	77	76
14	50	55	55	52	43	57	49	57	50	49	55	60
16	64	60	56	56	61	62	64	51	61	60	55	60
17	49	40	40	43	48	40	45	42	40	46	48	40
21	48	50	42	52	45	42	48	50	46	53	47	41
22	46	34	41	42	44	39	48	48	43	44	45	48
24	48	44	54	50	40	40	45	53	55	45	45	49
25	43	40	40	55	40	55	46	42	41	47	48	46
27	54	52	49	55	52	55	50	52	50	52	47	55
28	61	59	62	65	61	69	64	59	62	61	64	68
29	60	66	64	63	61	54	59	67	65	62	62	60
30	48	50	50	48	49	51	49	49	51	50	53	54
32	62	64	62	65	58	66	67	64	61	61	60	64
33	75	76	75	73	74	76	77	78	78	79	73	80
34	57	58	61	65	56	57	53	70	62	60	68	60
36	48	56	54	46	51	57	56	51	52	55	55	53
37	47	46	41	45	47	43	46	40	45	48	40	40
39	63	66	62	63	65	63	63	63	64	65	60	61
40	74	71	75	72	72	65	76	76	71	71	70	69
41	47	42	42	50	52	53	48	42	53	51	47	49
45	49	50	43	49	56	46	58	42	44	48	46	53
46	53	56	59	56	56	58	54	53	60	51	54	54

A4. Final Trial Number Task Comparison

	Fearful			Happy			Neutral		
Partic. Number	**ODD**	**ED**	**GD**	**ODD**	**ED**	**GD**	**ODD**	**ED**	**GD**
15	49	58	55	58	70	67	56	51	66
17	37	51	43	58	68	69	52	60	46
19	65	70	64	65	70	68	43	46	47
21	78	76	70	81	74	73	71	67	69
22	80	79	71	63	65	66	79	72	79
23	67	66	62	60	68	67	61	75	62
24	65	55	65	71	52	73	55	59	58
26	66	73	70	71	71	78	63	67	64
27	71	68	75	73	75	75	69	71	68
29	49	49	47	69	76	69	68	67	72
33	85	71	83	75	72	75	51	56	54
34	62	67	69	53	75	70	61	65	70
35	88	93	92	85	87	86	88	84	90
37	89	91	88	87	78	87	73	76	81
38	87	80	87	72	82	81	79	75	80
41	41	47	37	55	72	73	64	54	59
42	62	61	63	50	52	55	80	78	79
47	62	62	60	72	66	73	68	73	79
49	80	86	84	74	71	69	68	67	71
50	62	60	50	57	51	62	63	51	63
52	49	73	61	60	75	67	51	54	54
55	66	67	64	58	62	46	57	53	61
57	51	50	54	65	69	62	56	39	42
58	64	64	65	73	76	84	58	66	61
60	74	71	68	73	75	75	72	89	84
61	72	70	70	52	42	60	52	40	54
62	77	98	73	74	60	77	55	45	50
64	75	80	80	72	67	80	55	65	61
66	82	76	80	80	83	66	71	72	77